heterozygosity resulting from inbreeding probably increases vulnerability to pathogens and parasites.

If colonies are sessile how do they proliferate to form new colonies? There is an optimum size for colonies and a threshold beyond which larger group size is not beneficial, due to diminishing per capita prey returns. Excessive group size leads to colony fragmentation by budding. Daughter colonies are derived from a single parental source through a small foundling group, often a single gravid female. This means there are high levels of between-colony genetic variance. Colony fission can also occur, typically when a colony web collapses under its own weight or falling branches break the web.

What can we learn from social spiders? Sociality can enhance foraging, reproduction and protection from predation or parasites, but what factors facilitated the origin of inbred spider sociality? Social spiders are a fast-growing research area for studying the factors that encourage the evolution of sociality and those underlying the character of different social groups.

Where can I find out more?

Avilés, L., and Bukowski, T.C. (2006) Group living and inbreeding depression in a subsocial spider. Proc. Roy. Soc. B *273*, 157–163.
Avilés, L., McCormack, J., Cutter, A., and Bukowski, T. (2000) Precise, highly female-biased sex ratios in a social spider. Proc. Roy. Soc. B *267*, 1445–1449.
Bilde, T., Lubin, Y., Smith, D., Schneider, J.M., and Maklakov, A.A. (2005) Transition to social inbred mating systems in spiders: role of inbreeding tolerance in a subsocial predecessor. Evolution *59*,160–174.
Evans, T.A. (1999) Kin recognition in a social spider. Proc. Roy. Soc. B *266*, 287–292.
Vollrath, F. (1986) Eusociality and extraordinary sex ratios in the spider Anelosimus eximius. Behav. Ecol. Sociobiol. *18*, 283–287.
Whitehouse, M., and Lubin, Y. (2005) The functions of societies and the evolution of group living: spider societies as a test case. Biol. Rev. *80*, 347–361.

Computational Biology Group, Department of Computer Science, University of Sheffield, Sheffield S1 4DP, UK.
E-mail: drdejackson@yahoo.co.uk, duncan@dcs.sheffield.ac.uk

Primers

The social life of corvids

Nicola S. Clayton[1] and Nathan J. Emery[2]

Of the 120 species of birds in the corvid family, which includes the crows, ravens, magpies and jays, the bare-faced rook is perhaps the most social of them all. At a rookery in Norfolk, for example, winter roosts can number up to 60,000 individuals. The name for a congregation of rooks is a ‘parliament’. In English folklore, parliament is an apt name for rook justice, as it is said that rooks form a circle around a wrongdoer producing a cacophony of calls and caws which can go on for hours until the offender is either attacked and killed or released to live another day. Although only fiction, such tales reflect their canny reputation as thieves and tricksters, as well as possessors of great wisdom.

Like most birds, corvids are monogamous, and the core unit is therefore the mated pair. This pair bond is typically for life, and the pair remains together throughout the year. For example, rooks and ravens find a partner during the autumn months, taking part in impressive aerobatic displays and food sharing which may be to assess the quality of a potential mate. Once juvenile rooks and ravens pair, they engage in extensive mutual preening and bill twining (bill holding) and support one another in fights.

Variety is the spice of corvid social life

The details of corvid sociality vary from species to species, and even population to population (Table 1). For example, raven pairs prefer to nest in the privacy of their own large territory, whereas rook pairs find a micro-territory, a nest site within a large colony of tens or hundreds of individual nests, called a rookery. In both species, this territory (or micro-territory) is usually occupied for life. Once the juveniles become fully independent, they leave the natal area and sometimes join other juveniles to form ‘teenage’ gangs of vagrants. This behaviour has been well documented for ravens capitalising on food bonanzas.

Whilst raven pairs remain in their territory, rook pairs range alone until later in the year when they join massive winter roosts containing thousands of individuals. This social variation in rooks, as well as other colonial corvids such as pinyon jays, is suggestive of the fission–fusion societies of chimpanzees, dolphins and spider monkeys. Indeed, seasonal changes in pinyon flock composition are even more complex, demonstrating higher levels of fission–fusion as jays dispersing from neighbouring colonies will join other flocks. Whilst juvenile ravens and rooks form gangs themselves after leaving their parent’s territory, pinyon jay offspring form crèches with the offspring of other adults. These crèches are fed and protected by a subset of adults whilst others go off to forage, which probably has had a significant effect on their later socialization. So one of the hallmarks of corvid sociality is behavioural flexibility, and consequently there is considerable variation not only between species but within a species, because of seasonal and ontogenetic changes in the size and composition of the social network.

Perhaps the classic case of corvid sociality is the communal cooperative breeding of the Florida scrub-jay. In this system, there are small family groups rather than a large colony. The young are raised not only by the parents, but also by non-breeding relatives, called ‘helpers at the nest’. Such helpers aid in feeding the offspring, but also help in defending the nest and keep a look out for predators. Helping appears to be highly dependent on environmental conditions, and is consequently found in sparse habitats where there are

Table 1. The breadth and depth of corvid social lives.

Species	Level of sociality	Cooperative breeding?	Breeding unit	Nest spacing	Seasonal pattern of territory occupancy	Foraging areas
Rook	Colonial pairs	No	Single pair	Aggregated	Breeding season (but also nest repair in autumn and winter)	Outside territory, usually on agricultural land
Raven	Territorial pairs	No	Single pair	Even	Year round	Within territory
Jackdaw	Colonial pairs	No	Single pair	Aggregated	Year round	Outside territory, usually on grassland
Carrion crow	Territorial pairs	Generally no[1]	Single pair	Even	Year round	Within territory (during breeding season), range extended outside breeding season
Black-billed magpie	Territorial pairs[2] Non-territorial pairs[3]	No	Single pair	Even[2] Aggregated[3]	Year round[2] Breeding season[3]	Within territory[2] <400 m from nest[3]
Yellow-billed magpie	Colonial pairs	No	Single pair	Aggregated	Year round	Within territory and communal flock area
Clark's nut-cracker	Territorial	No	Single pair	Even	Year round	Outside territory; large range
Pinyon jay	Colonial	Yes	Multiple pairs (typically 50)	Aggregated	No territoriality	Not applicable
Western scrub-jay	Semi-territorial[4]	Generally no[5]	Single pair	Even	Year round	Largely within territory
Florida scrub-jay	Territorial small family groups	Yes	Single plus helpers	Even	Year round	Within territory
Mexican jay	Territorial small family groups	Yes	Two pairs plus helpers	Even	Year round	Within territory

[1]In Switzerland, carrion crows do not breed cooperatively; however, in the arid areas of Spain cooperative breeding is common. [2]European populations. [3]North American populations. [4]Higher degree of sociality with territorial groups including >3 birds. Frequent interactions with neighbouring territory holders and prolonged associations with some juvenile non-breeding vagrants may result in more complicated social networks. [5]Throughout the western US, western scrub-jays do not breed cooperatively; however; helping behaviour has been detected in some southern-most populations; in Mexico cooperative breeding is common in arid areas.

fewer opportunities for young birds successfully to set up their own territories and raise their own young. Further evidence in support of this comes from the fact that in a closely related species, the Western scrub-jay, and a more distantly related species, the carrion crow, there are geographic differences in the prevalence of helping behaviour. In the lush Central Valley of California, scrub-jays primarily live in pairs accompanied by juveniles without territories of their own, whereas in harsher climes, such as Mexico, scrub-jays live in extended family groups with helpers at the nest, just like their sister species the Florida scrub-jay. In the case of carrion crows, it is clear that these variations are not due to genetic differences between populations, but a consequence of differences in habitat. In sparse environments the young birds stay in the natal territory and help rear their parents' young; but in years when adult mortality is high, the juveniles desert to establish their own territory.

The Mexican jay is perhaps one of the more extreme cases of this communal cooperative breeding system, as typically two adult pairs share a territory along with various non-breeding helpers, all of whom take part in feeding the young and defending the nests. The differences in social system led Jerram Brown to suggest that there are two alternative routes to sociality in the New World jays; either by progressive overlapping of home ranges together with a reduction of aggressive spacing leading to coloniality, or retention of the young in the territory for increasingly longer periods of time resulting in a communal social structure. We suggest that this evolutionary scenario can in fact be applied to the entire family Corvidae, and we give some examples in Figure 1. Given the prevalence of sociality within most of the corvids which have been studied to date, we think that there is good reason to believe that the common ancestor of the corvids was social. Even in species such as the Clark's nutcracker, which has a relatively simple social structure, family groups may come together in loose flocks once the young have fledged.

Relationships in the roost

As we argued in the last section, although corvids generally display great flexibility in their social lives, the core unit is the pair-bond. These life-long, year-round partnerships have important implications for corvid social behaviour. Typically, monogamous birds form pairs in order to raise offspring together and defend their nest; but at the end of the breeding season, the pairs will often split and form new pairs the next year. However, in the case of some corvids, notably rooks and jackdaws, the pairs remain together throughout the year and return to the same nesting site year after year. It is thought that these long-term partnerships resemble the long-term alliances of many primates and dolphins. For example, the relationship between pair mates

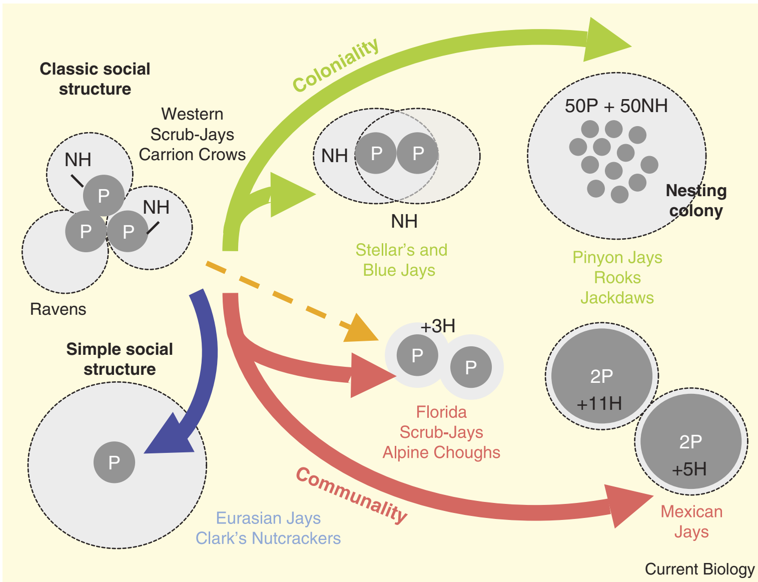

Figure 1. Alternative routes to sociality in Corvidae.

Corvids either evolved social groups based on coloniality (green line, for example, pinyon jays, rooks and jackdaws) or communality (red line, for example, Florida scrub-jays, Alpine choughs and Mexican jays), whereas simpler social systems, such as that displayed by Eurasian jays and Clark's nutcrackers, suggest secondary reduction of social complexity (blue line). Some species, such as carrion crows and western scrub-jays, may display characteristics of a cooperative breeding society in some environmental conditions (dotted orange line). Dark grey circles represent pair territories, whereas light grey circles represent pair home ranges. P, breeding pair; H, non-breeding helper; NH, non-breeding non-helper. (Adapted from Brown (1974).)

is established and reinforced through mutual preening and food sharing, and they enhance their dominant status by aiding one another in fights against third parties. In this way, pairs may increase their access to resources that would generally be unavailable to them as singletons. For example, jackdaws form pairs within the first year, probably because good nest sites are difficult to find and there is intense competition for sites with other pairs. Only a strong coordinated partnership has the ability to defend sites against other pairs.

Corvids are known for their relatively long period of development, typically several months, before becoming truly independent from their parents. Even so, many young corvids, including rooks and jackdaws, form selective partnerships soon after they start feeding themselves. In the first instance, these are not necessarily with individuals of the opposite sex. In a captive group of rooks, we observed the formation of opposite-sex and same-sex pairs around three months of age. Once the birds became sexually mature, the same sex pairs swapped partners, presumably in preparation for breeding. The individuals in the pairs were strongly affiliative and demonstrated no aggression to one another, in stark contrast to the aggression they directed to other individuals. The behaviour of the pairs was mutualistic, as both members benefited from the partnership, both gaining dominance and both helping one another in fights.

Social life has costs as well as benefits. In the competition for resources, it is inevitable that individuals will fight. The larger the social group, the more opportunities there may be for conflict. Consequently, members of a pair engage in a number of tactics to manage the stress associated with aggression and minimise the risk of damaging the partnership. This occurs with active social support either through direct aggression towards the same third party as the partner or direct affiliation towards their partner after they have been the victim or winner of a fight.

Both cases are examples of cooperative behaviour, which probably helps maintain social bonds, but in the case of post-conflict affiliation is also important in stress management. If one member of a pair takes part in an agonistic encounter with a third party, either they retreat to their partner after the fight has ended or their partner moves towards them, producing a special affiliative behaviour, bill twining, which is sometimes also called bill holding (Figure 2A). Similar behaviours, such as kissing and embracing, have been reported for chimpanzees after fights. Other examples of affiliative behaviours are preening (Figure 2B), food sharing (Figure 2C), and the bowing and fanning display (Figure 2D).

One major difference from chimpanzees is the total absence of reconciliation between former antagonists. It has been suggested that reconciliation only occurs between individuals that have a valuable relationship; such as alliance partners in chimpanzees and life-long pair bonded corvids. We found no evidence that rooks fight with their partners or form affiliations with other colony members, which is probably why there is apparently no need for the birds to repair relationships with other parties.

The ability to recognise individuals is an essential precursor for maintaining affiliative relationships, understanding relationships between third parties and classifying individuals based on their social class — parent, sibling, mate, friend, foe or group member. It is particularly important in stable social groups or fission–fusion societies, where individuals may rejoin the group at unpredictable times. Research in a number of corvids has found that they classify individuals based on various social categories. Mexican jays responded to calls played on a speaker with a shorter latency, and came close to the speaker more frequently when the calls were from members of the nearby group compared to when they were from members of their own group, suggesting that they could discriminate between the two. Corvids begin to recognise one another very early in development. Sibling rooks, for example, recognise one another by their calls before fledging, whereas adults can recognise one another by their visual appearance alone.

How does recognition occur? One possibility is that individual vocalizations contain a 'signature' which is unique to that particular individual in the same way that the configuration of faces is unique to each individual. It has been suggested that this form of categorization occurs through intense socialization with individuals of a particular social class. By this process, individuals which are either strongly bonded, such as monogamous pairs or siblings or parents and offspring, spend a long time in proximity and rapidly learn the physical and/or vocal attributes of that specific individual. In the realm of vocalization, pair-bonded individuals often converge on the same call structure. Vocal sharing occurs with the warble vocalizations within groups of Australian magpies, where magpies in the same group share more warble syllables than magpies of different groups (a similar system occurs for the non-territorial song of American crows).

Figure 2. Photographs of rook affiliative behaviours.
(A) Bill twining or bill holding. (B) Allo-preening. (C) Food sharing. (D) Bowing and fanning display. (Photographs: Chris Bird.)

What do crows know about what crows know?

In large social groups with a linear dominance hierarchy, such as many corvid societies, the ability to make inferences about the relative status of individuals within this hierarchy is an important skill, often called transitive inference. For example, if Bob is more dominant than Joe, and Joe is more dominant than Simon, and Bob and Simon have a fight, what would be the predicted outcome? Transitive inference allows an animal to calculate that Bob should out-compete Simon even though Bob and Simon may previously never have interacted.

When an arbitrary version of the transitive inference test was presented to social pinyon jays and less social western scrub-jays in the laboratory, the pinyon jays outperformed (learned more quickly than) the scrub-jays. But the scrub-jays did learn the task and with a similar learning curve to the pinyon jays. Pinyon jays have also been tested on a social version of this test. Birds were split into groups, and allowed to observe contests for food between pairs of jays of known dominance from either the same or a different group. For example, bird B was paired with bird A, from the same group (A was dominant to B), or with bird 2 from a different group (birds in the 'letter' group were dominant to birds in the 'number' group). The observing jay, bird 3, subservient on previous encounters to bird 2, was then allowed to compete with bird B. As bird B was submissive to bird A, but dominant to bird 2, if bird 3 formed a representation of the relative dominance of those birds from the observed encounters, then it should display a greater number of submissive displays to B. This was exactly what they did across many combinations of birds from different groups which had never interacted before.

Corvids which live in large, complex social groups have to solve specific social problems associated with competing with others for scarce resources. Transitive inference, recognising third party relationships and tactical deception are potential weapons in the social corvids' cognitive arsenal. However, the social problems faced by less social corvids are not necessarily less complex. Take caching, for example. Many avian and mammalian species hide food, using memory to accurately retrieve their food caches later. For most species, the problems associated with finding hidden food are personal problems. But for caching corvids, the problems are exacerbated by the fact that corvids can remember the location of not only their own caches, but also the caches of others. This observational spatial memory has been suggested to be the cornerstone of how corvid pilferers can steal food without aggressive retaliation from the 'owner' of the cache. Corvid cachers therefore need to protect their caches from the possibility of theft when they have left the cache site, as well as protecting their caches aggressively when potential thieves are present. Studies of western scrub-jays and ravens have been particularly illuminating in regard to the cognitive mechanisms involved in protecting caches from conspecifics, and whether such mechanisms may involve the attribution of mental states.

When confronted with a potential thief, ravens and scrub-jays will attempt to cache as far as possible from the eyes of the competitor, hide caches out of sight — behind rocks, trees or other barriers — and scrub-jays will even cache in darkened areas rather than sites that are well lit. Such skills suggest visual perspective taking — computing what another can or cannot see. If the situation does not allow the storers to avoid a pilferer's gaze, they will return to their caches at a later time and move them to new places of which the observer was not aware. These protective behaviours are not born with the cachers, they are triggered by experience. In a study of captive scrub-jays, only cachers that had the previous experience of being thieves themselves implemented this strategy of moving their caches to new places, whereas naïve scrub-jays left their caches to their fate at the beaks of the observers.

Although adult scrub-jays and ravens do not live in extended social groups, they must have the ability to recognise individuals. Indeed, when confronted with observers of different identities, they only used cache-protection strategies when the earlier observer was a dominant jay. They did not use protective strategies when the observer was their partner or a subordinate. When cachers hid food in different places in front of different observers — for example, when they cached in tray A in front of observer A, and cached in tray B in front of observer B — and they were allowed to recover their caches, in front of either the same two observers or a naïve observer who had not seen the caching, the cachers selectively retrieved those caches from the specific tray in which they had cached in front of a specific observer. They retrieved caches from tray A in front of observer A, but left the other caches alone, so not revealing their location. They did not recover any caches in front of the naïve jay, but recovered a majority of their food when allowed to recover in private. Interestingly, when they recovered in front of either observer, A or B, they moved their caches around multiple times, an avian version of the 'shell game'. These behaviours are shared with ravens, although it is not yet clear whether these species really recognise the different knowledge states of individuals or they are just responding to subtle behavioural cues of the observer.

Not all things are bad in the social lives of corvids. There are benefits for living in a social group outside of the traditional reasons, based on defence against predators or foraging opportunities. One suggestion is that corvids may even be cultural animals. Life in a social group allows the individuals within that group to learn things from others that are either too dangerous for them to learn themselves or too time consuming. Rooks, for example, use social information to locate profitable foraging sites on agricultural land, and in the lab have been shown to exploit novel food sources based on the feeding preferences of conspecifics. Although corvids have yet to be tested for the extent of their social learning abilities, social learning has been suggested to have played a significant role in the spread of the tool manufacture specializations of New Caledonian crows. Laboratory studies suggest that young crows do not appear to require social stimulation to begin using and making tools, but the distribution of different tool types across New Caledonia has been raised as a potential example of cultural variation. The 'simplest' tools are found across the island, whereas waves of complexity appear to have spread to pockets across the island. It remains to be determined whether such variability really is a cultural trait or the result of innovation or trial and error learning.

We have described a very small subset of the variety of social organization, social behaviour and social cognition of the Corvidae, and much remains to be learned. There are over 120 species of corvids, and yet few have been systematically studied in the lab or the field. We are therefore completely ignorant of the social lives of most of the extant corvids. This article therefore remains a work in progress with exciting prospects ahead, and we hope that this primer, along with the recent suite of studies on the corvids, might inspire more researchers to study these fascinating creatures.

Further reading

Brown, J.L. (1974). Alternative routes to sociality in jays — with a theory for the evolution of altruism and communal breeding. Am. Zool. *14*, 63–80.
Clayton, N.S., Dally, J.M., and Emery, N.J. (2007). Social cognition by food-caching corvids: the western scrub-jay as a natural psychologist. Phil. Trans. R. Soc. Lond. B *362*, 507–522.
Emery, N.J., and Clayton, N.S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. Science *306*, 1903–1907.
Emery, N.J., Seed, A.M., von Bayern, A.M.P., an Clayton, N. S. (2007). Cognitive adaptations of social bonding in birds. Phil. Trans. R. Soc. Lond. B *362*, 489–505.
Goodwin, D. (1986). Crows of the World (Second edition). British Museum (Natural History): London.
Heinrich, B. (1999). Mind of the Raven (New York, NY: Harper Collins Publishers).
Heinrich, B., and Bugnyar, T. (2007). Just how smart are ravens? Sci. Am. *296*, 46-53.

[1]Department of Experimental Psychology, University of Cambridge, Cambridge CB2 3EB, UK.
[2]Sub-department of Animal Behaviour, University of Cambridge, Cambridge CB3 8AA, UK.
E-mail: [1]nsc22@cam.ac.uk, [2]nje23@cam.ac.uk