



The social structure of New Caledonian crows

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ARTICLE INFO

Article history:

Received 16 February 2010
Initial acceptance 19 April 2010
Final acceptance 9 September 2010
Available online xxx
MS. number: 10-00117

Keywords:

Corvus moneduloides
extended parental care
New Caledonian crow
social intelligence
social structure
technical intelligence
vertical transmission

New Caledonian (NC) crows, *Corvus moneduloides*, have impressive tool-manufacturing and tool-using skills in the wild, and captive birds have displayed exceptional cognitive abilities in experimental situations. However, their social system is largely unknown. In this study we investigated whether the social structure of NC crows might have had a role in the development of their cognitive skills. We observed crows in their natural habitat on the island of Maré, New Caledonia, and estimated their social network size based on tolerance to family and nonfamily crows at feeding tables. Our findings suggest that NC crows are not a highly social corvid species. Their core unit was the immediate family consisting of a pair and juveniles from up to two consecutive breeding years. Pairs stayed together year round, and were closely accompanied by juveniles during their first year of life. Parents were highly tolerant of juveniles and sometimes continued to feed them well into their second year. NC crows predominantly shared feeding tables with immediate family. Of the nonfamily crows tolerated, juveniles were overrepresented. The main mechanism for any social transmission of foraging skills is likely to be vertical (from parents to offspring), with only limited opportunity for horizontal transmission. The social organization we found on Maré is consistent with the idea that NC crows' multiple pandanus tool designs on mainland Grande Terre are an example of cumulative technological evolution.

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Two main hypotheses have been proposed to explain how complex cognitive abilities have evolved. The social intelligence hypothesis claims that social pressures have driven the evolution of a flexible, intelligent mind (Byrne & Whiten 1988; Whiten & Byrne 1997; Dunbar 1998). This hypothesis is supported by many findings that correlate brain size with group size and complexity of social relationships in primates and a range of other mammals (Byrne & Bates 2007). However, no clear correlation has been found between avian brain size and sociality (Emery et al. 2007). Byrne & Whiten (1988) suggested that the type and quality of social relationships might be more important factors for predicting intelligence than group size (see also Emery et al. 2007 in relation to birds). In contrast to the social intelligence hypothesis, the technical intelligence hypothesis states that ecological factors, in particular the need for extractive foraging, helped drive brain expansion and the associated increase in cognitive abilities (Byrne 1997). This theory is supported by findings that correlate the size of forebrain areas of both birds and primates with flexible and innovative nonsocial behaviours such as tool use (Lefebvre & Sol 2008). The technical intelligence hypothesis was proposed as a mechanism

that might work alongside the social intelligence hypothesis to drive the evolution of intelligence (Byrne 1997).

Corvids are renowned for their innovative behaviour, relatively large brains and general intelligence (Emery 2004; Emery & Clayton 2004a, b). For example, New Caledonian (NC) crows, *Corvus moneduloides*, have the most complex tool-manufacturing abilities among nonhuman animals, including primates (Hunt 1996; Hunt & Gray 2004a, b). Hunt & Gray (2003) suggested that the design diversification of the tools that NC crows make on mainland Grande Terre from *Pandanus* spp. leaves might be the result of cumulative technological evolution. Although tool use is not necessarily indicative of specialized cognition (Beck 1980), NC crows have demonstrated impressive abilities when solving complex physical problems in captivity. They can modify novel tool material in appropriate ways (Weir et al. 2002; Weir & Kacelnik 2006), spontaneously solve a novel metatool task (Taylor et al. 2007, 2010) and appear to reason about interactions between objects (Taylor et al. 2009a, b). Their metatool performances rival those of the great apes (Köhler 1925; Mulcahy et al. 2005). With the possible exception of rooks, *Corvus frugilegus* (Bird & Emery 2009), they appear to be the only nonhuman species known to have solved problems requiring tool use through causal reasoning (Martin-Ordas et al. 2008; Seed et al. 2009; Taylor et al. 2009a, b). Furthermore, NC crows also possess relatively large brains compared to other birds (Cnotka et al. 2008; Mehlhorn et al. 2010). However, very little is known about their social structure. Early observations suggested

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that NC crows live mostly in small family groups (Hunt 2000; Kenward et al. 2004). Hunt (2000) observed a nutritionally independent juvenile moving around with adults and suggested that the 30 or more crows he observed in a tree at Saraméa on Grande Terre were a temporary aggregation of small groups. Kenward et al. (2004) observed NC crows flying above the canopy on Grande Terre in groups of typically three to four and captured crows in small mixed-sex groups, which is consistent with the idea that NC crows mostly live in small family groups. A more intensive study on the island of Maré showed that juveniles follow their parents for at least a year and are frequently fed during this time (Holzhaider et al. 2010). However, there has been no detailed field study with individually marked NC crows to investigate their social structure.

The family Corvidae displays a very broad range of social organization (dos Anjos et al. 2009). Corvids tend to be monogamous with pairs usually remaining together year round, and pair bonds often last for life. Nevertheless, social organization ranges from solitary pairs that nest within a large territory (e.g. common ravens, *Corvus corax*; Heinrich 1999) to highly social species (e.g. the pinyon jay, *Gymnorhinus cyanocephalus*, which lives in stable groups of up to 500 birds and breeds cooperatively within the colony; Marzluff & Balda 1989). If, as Hunt (2000) and Kenward et al. (2004) suggested, NC crows live mostly in small family units it would place them at the lower end of corvid social complexity and increase the possibility that physical cognition related to tool use had a role in the evolution of their impressive cognitive abilities. In this study, we present the results of 4 consecutive years of observations on a wild population of individually colour-banded NC crows on the island of Maré, New Caledonia. We describe the structure of nine target families, their breeding behaviour and the tolerance between crows at feeding sites.

METHODS

Our study was carried out on the island of Maré, New Caledonia, about 5 km inland from Wabao village. We observed crows from August to December 2003, June to December 2004 and in most months in 2005 (January–May, July and October–December) and 2006 (January–May, August and October–December). The study area consisted of ca. 1.5 km² of primary and secondary rainforest interspersed with garden patches where local villagers grew fruit and vegetables. These gardens were usually used for 2 consecutive years before they became overgrown. Crows foraged in both forest and the garden patches.

We documented the social structure of nine target families that consisted of a total of 28 individual crows (Table 1). All but one of these 28 birds was fitted with coloured leg bands for individual identification. We captured crows using a 8 m × 4 m 'whoosh net' obtained from SpiderTech Bird Nets, Helsinki, Finland. From 2003 to 2006 we individually colour-banded many more crows at the site, but we knew little about the families of these other birds. We recorded adult crows as being partners if we observed them together at any of the following activities: courtship feeding, nesting, and feeding the same juvenile. We identified parent–juvenile relationships by parental feeding, intensive begging and prolonged following of an adult by a juvenile.

Observations were made at 22 feeding tables distributed throughout the study area (Fig. 1). Feeding tables were ca. 1 m above the ground and made out of wood found in the vicinity. On these tables we placed dead logs in which we drilled vertical holes. In these holes we placed meat that could only be extracted with tools. We usually provisioned the tables with fresh papaya and positioned a *Pandanus* sp. tree ca. 2 m high next to each table to

Table 1
Details of target families

| | Crow | Status | Sex | Hatched | Fledged | Banding date |
|----------|---------|----------|-----|--------------|-------------|--------------|
| Family 1 | r/* | Adult | M | — | — | 23 Sept 2003 |
| | Pandora | Adult | F | — | — | Unbanded |
| Family 2 | y/wy | Juvenile | M | 2 Dec 2004† | 1 Jan 2005 | 30 Dec 2004 |
| | l-g/r | Adult | M | — | — | 21 Sept 2003 |
| Family 3 | Pandora | Adult | F | — | — | Unbanded |
| | y/or | Juvenile | M | 13 Nov 2005† | 14 Dec 2006 | 13 Dec 2006 |
| Family 4 | o/y | Adult | M | — | — | 23 July 2004 |
| | -/go | Adult | F | — | — | 24 July 2004 |
| Family 5 | gy/l-g | Juvenile | M | 6 Nov 2005† | 6 Dec 2005† | 14 Feb 2006 |
| | oy/r | Juvenile | M | 6 Nov 2005† | 6 Dec 2005† | 14 Feb 2006 |
| Family 6 | o/- | Adult | M | — | — | 14 Sept 2003 |
| | -/g | Adult | F | — | — | 14 Sept 2003 |
| Family 7 | bo/- | Juvenile | F | 6 Nov 2005† | 6 Dec 2005† | 16 Feb 2006 |
| | y/b | Adult | M | — | — | 20 Sept 2003 |
| Family 8 | l-g/b | Adult | F | — | — | 2 Dec 2005 |
| | Moro | Juvenile | M | 6 Nov 2005† | 6 Dec 2005† | Unbanded |
| Family 9 | -/w | Adult | M | — | — | 14 Sept 2003 |
| | r/b | Adult | F | — | — | 14 Sept 2003 |
| Family 7 | -/oy | Juvenile | M | Dec 2003‡ | Jan 2004‡ | 23 July 2004 |
| | o/o | Juvenile | F | 7 Dec 2004† | 2 Jan 2005 | 30 Dec 2004 |
| Family 8 | -/wy | Adult | M | — | — | 23 Sept 2003 |
| | gw/b | Adult | F | — | — | 18 Oct 2004 |
| Family 9 | b/r | Juvenile | M | Dec 2003‡ | Jan 2004‡ | 24 July 2004 |
| | r/o | Juvenile | M | Dec 2003‡ | Jan 2004‡ | 18 Aug 2004 |
| Family 8 | y/g | Adult | M | — | — | 20 Sept 2003 |
| | g/y | Adult | F | — | — | 4 Aug 2005 |
| Family 9 | g/r | Juvenile | M | Dec 2004† | Jan 2005‡ | 4 Aug 2005 |
| | r/y | Adult | M | — | — | 19 Sept 2003 |
| | b/g | Adult | F | — | — | 19 Sept 2003 |

M = male, F = female.

* Predated in December 2004 before y/wy fledged.

† Date estimated from observations at the nest.

‡ Date estimated from mouth colouring and behaviour at capture.

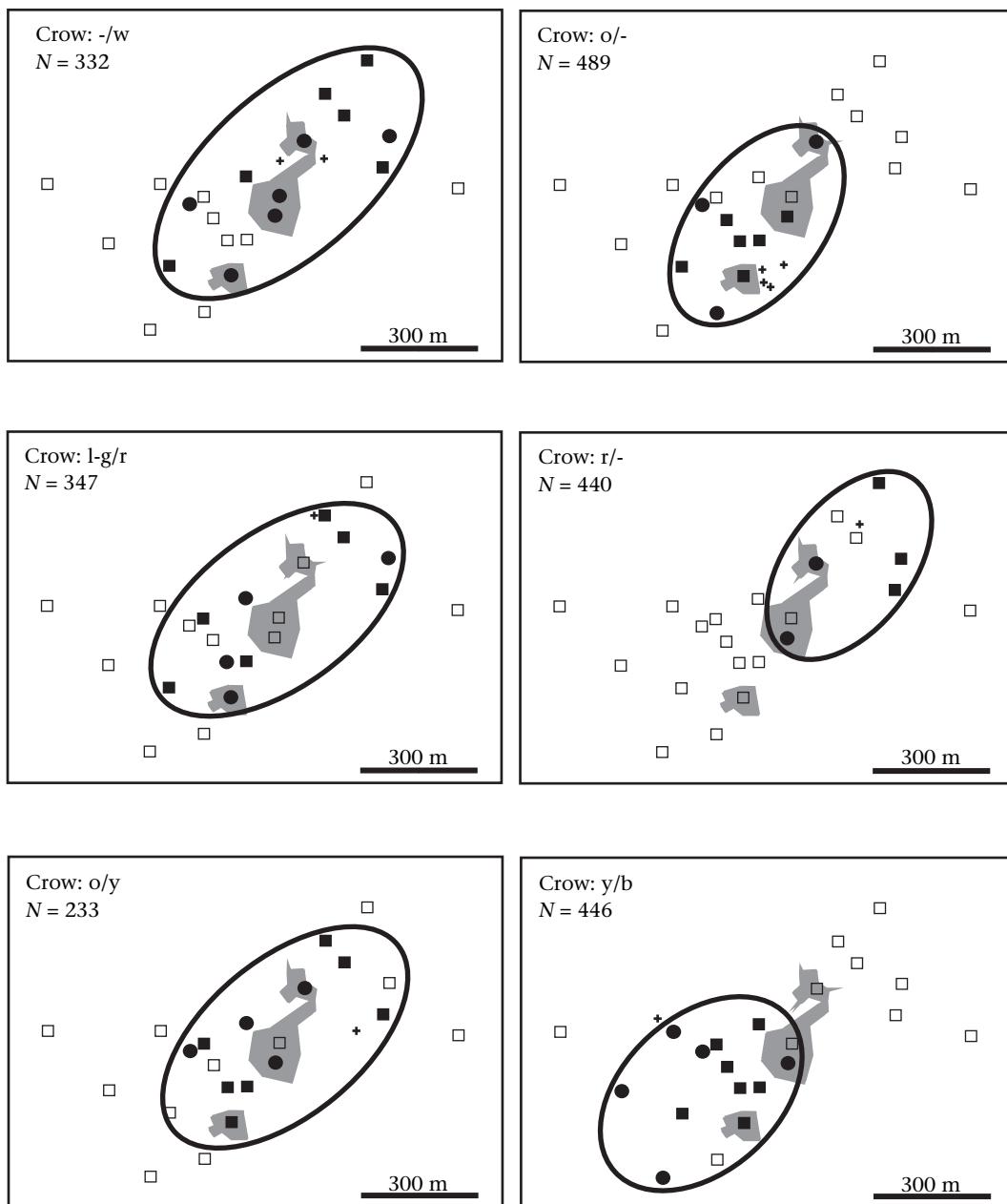


Figure 1. Foraging range of six target males based on observations at feeding tables. Squares and circles indicate the locations of 22 tables: empty square = no observations; black square = tables where we obtained video footage of visits; black circle = tables where we only obtained nonvideotaped data. The large black oval rings enclose all the tables where a crow was observed. The black crosses indicate the nesting site(s) of the respective males. Two large cleared areas associated with slash and burn gardening are shown by the shaded shapes. The sample size for each male is the total number of visits to the tables. North is at the top of the figures.

provide an opportunity for pandanus tool manufacture. The trees were obtained from surrounding forest and their trunks were secured to tables with string, with the leaf crowns above the table tops. We usually baited several tables at the same time, and the combination of tables baited at any one time varied. The presence of meat in the holes in a log usually initiated tool use by visiting crows.

Whenever one or more crows landed on a table we recorded the time of the visit and the individuals that were present. Visits were separated by at least 2 min when no crow was on the table. Although a 2 min interval was relatively short, on only a small percentage of occasions did we record more than one visit to a particular table by the same crow within a 10 min period (ca. 3% of all observations across target males in families 1–6). Therefore,

a crow that had visited a table to feed, or found no food present, usually went elsewhere to forage before returning. Visits were recorded in notebooks, videotaped with a hand-held camera, or videotaped remotely in conjunction with a motion detector (Wachit VMD-19M video motion detector, Farco Technologies, Rolleston, New Zealand). Whenever we observed a target bird away from tables we also recorded the location, time and whether a family member was present.

To determine whether pairs stayed together year round, we used (1) chance observations away from feeding tables when walking around the study area, (2) observations at feeding tables and (3) radiotracking data. We analysed the data collected in points 1 and 2 above in two ways. First, we looked to see how frequently partners were together in each month of the year. We counted the

days per month on which we had observed each target male (excluding radiotracking data). Then we counted on how many of those days we had observed the male at least once with its partner. If a target male was observed in more than 1 year we averaged the monthly data across years. For each month, we averaged the percentage of time that each male was observed with its partner. We excluded a male from monthly data if the sample size for the total number of days observed was less than 3. We also required data for at least two males in each month to allow the calculation of a mean. We applied a similar procedure to document the association over time between juveniles of the target families and their parents. Second, we analysed all observations at and away from feeding tables (excluding radiotracking data) to get the percentage of total observations that partners were seen at the same location. This meant that we often had multiple records per day for the same bird. Finally, in 2004 we radiotracked five of the nine target families as a check on the behaviour of birds at feeding tables (Table 2). To do this, we radiotagged either the male (r/-, o/-, -/wy and r/y) or the female (r/b) of the breeding pair. The radiotransmitters and associated weak-link harnesses (made by Sirtrack Ltd, Havelock North, New Zealand) had a total weight of ca. 6 g, which was 2.2% of the bodyweight of the smaller female crow r/b. We tracked the five crows using a hand-held Yagi directional antenna attached to a TR-4 receiver. We followed a particular crow for one session per day over usually several hours; sessions were both in the morning and afternoon to detect any differences in diurnal behaviour. When we observed the radiotagged crow directly we noted its behaviour and the presence of any other crows nearby. We removed the transmitter from o/-, it fell off r/b and r/- was predated with its transmitter still fitted. We could not capture -/wy and r/y to remove their transmitters, but we know the birds were still fully active at the study site in 2006. To our knowledge, the harnesses had minimal adverse effects on a crow's day-to-day behaviour, even over the long term. We only present here a qualitative account of the radiotracking observations.

Food sharing has been suggested to play an important role in the development of social bonds in other corvids such as jackdaws, *Corvus monedula*, (von Bayern et al. 2007) and rooks (Emery et al. 2007). Our feeding tables were highly desirable food sources where crows could feed together in close proximity. Therefore, to obtain a measure of NC crows' social network size we used tolerance at feeding tables. We analysed all videotaped visits to feeding tables of the six target males for which we had sufficient data, and recorded the number of both family and nonfamily birds with whom they shared tables. Family members were partners and any offspring. We recorded that a target male tolerated another bird if he allowed it to stay on the table or attached *Pandanus* sp. tree while he was also present. We applied the same procedure to assess the opportunity of first-year juveniles to observe tool use and manufacture at tables.

Social transmission in a population may be from parents and close family to offspring or between distantly related individuals. For transmission between distantly related individuals, some authors distinguish between horizontal transmission (between

peers, i.e. individuals from the same (F1) generation) and oblique transmission (between distantly related individuals of different generations; Boyd & Richerson 1985; Findlay et al. 1989; Allison 1992). Our objective was to determine the potential opportunity for juveniles to learn tool skills socially from both immediate family members and nonfamily individuals. We therefore defined transmission to a juvenile from its parents and older siblings as 'vertical', and transmission from any other crows as 'horizontal' (Cavalli-Sforza & Feldman 1981; Bisin & Verdier 1998). A juvenile had the potential opportunity to learn tool skills both via vertical and horizontal transmission at feeding tables.

In late 2004, we also observed four breeding pairs at their respective nests (families 1, 4, 6 and an additional pair). To observe nests, we set up raised hides at a distance of 10–20 m away. To minimize disturbance of the breeding pairs we observed each nest only every 2–3 days for several hours. We recorded the amount of time each parent spent sitting on the nest and if it fed the juvenile (s). To estimate the maximum duration of parental feeding post fledging, we recorded the approximate age (months) when each juvenile in families 1–8 was last observed being fed by one of its parents. For this analysis we only included families in which we observed both the juvenile and its parents for at least 12 months post fledging.

The research reported in this paper was approved by the University of Auckland Animal Ethics committee and complies with the laws of New Caledonia.

RESULTS

Breeding and Parental Care

NC crows at our study site began breeding around November, when both partners contributed to nest building. In 2004, we observed each nest of four breeding pairs for a mean \pm SE of 21.4 ± 3.24 h ($N = 4$) from the start of incubation until juveniles fledged or the nest was deserted. Nests were built ca. 3–8 m above ground, but still well below the canopy. Females laid two or three eggs and incubation lasted ca. 18 days (mean \pm SE = 17.67 ± 0.33 days, $N = 3$; families 1, 4 and 6). Only females incubated and brooded chicks, but males fed brooding females regularly on or close to the nest. From a total of nine chicks hatched by the four pairs, only two survived to fledging (22%). The two surviving chicks left the nest 26 and 30 days after hatching. One pair built a replacement nest and started incubating after both chicks of the first brood had died, but the second nest also failed. Reasons for chick mortality appeared to be mostly adverse weather conditions and predation. For example, in 2004 we observed a goshawk, *Accipiter* sp., attack the two chicks that Pandora was raising alone after her partner (r/-) was apparently killed by a goshawk. We also found nests in 2003 (family 4) and 2005 (families 2, 4 and 6); nests of the same family were never more than 100 m apart (Fig. 1).

Juveniles were fed by both parents. Although parental feeding frequency clearly declined after about 6 months (Holzhaider et al. 2010), juveniles continued to be fed infrequently until at least the beginning of the next breeding season. The average age \pm SE of a juvenile when we last observed it being fed was 12.6 ± 2.4 months ($N = 5$). We observed three juveniles over 12 months of age from different families begging vigorously and subsequently being fed (at 14, 14 and 20 months). At 20 months of age, we observed -/oy being fed by both his parents even though they were raising a new juvenile. We never observed any bird other than the biological parents feeding juveniles or contributing directly in any other way to their upbringing.

Table 2

Summary of radiotracking effort on five adult crows

| Crow | Family | Tracking period | Tracking sessions | Mean hours \pm SE tracked per session/day |
|------|--------|-----------------------------|-------------------|---|
| r/- | 1 | 7 Sept 2004 to 18 Nov 2004 | 15 | 3.82 \pm 0.17 |
| o/- | 4 | 17 July 2004 to 17 Nov 2004 | 25 | 3.62 \pm 0.17 |
| r/b | 6 | 8 Sept 2004 to 13 Nov 2004 | 26 | 2.74 \pm 0.15 |
| -/wy | 7 | 10 Sept 2004 to 5 Jan 2005 | 34 | 2.92 \pm 0.17 |
| r/y | 9 | 8 Sept 2004 to 11 Jan 2005 | 17 | 3.45 \pm 0.23 |

Pair Bonding and Family Structure

We found that breeding pairs remained together over the long term. The mated pairs in seven of the nine families (Table 1) were observed together for a mean \pm SE of 3.03 ± 0.63 years ($N = 7$; Table 3). Pandora's pair bond with r/- ended in 2004 when r/- was killed. However, the remaining six pairings continued past the date that we last saw each pair together. Two pairs (l-g/r and Pandora; o/- and -g) were together over four and five consecutive breeding seasons, respectively. In 2005, Pandora paired with a new partner (l-g/r) several months after her former partner (r/-) had been killed. Although we never observed l-g/r feeding his 'stepson' y/wy, he tolerated him on feeding tables and rarely showed any agonistic behaviour towards him. Because l-g/r accepted y/wy, we included y/wy in both families 1 and 2.

Observations at feeding tables and radiotracking data were consistent with mated pairs remaining together throughout the year on the same foraging range. As females tend to be reticent and visited tables less frequently than males (see above), we probably underestimated the amount of time pairs travelled together. When we limited records per bird to one per day at or away from feeding tables, we also found that pairs travelled together year round (Fig. 2). This was supported by female partners being observed with their respective target male on average 39.2% of the time that the males were seen (Table 4). Furthermore, both partners had the same foraging range, and the foraging ranges of pairs differed (Fig. 1). For the six target males in Fig. 1, the foraging ranges of their partners (as documented at feeding tables) never went outside the respective males' ranges (indicated by the large oval rings). Only one female (r/b) used a table not used by its partner. Four of the six target males in Fig. 1 used tables not used by their partners (-w: $N = 2$ tables; o/-: $N = 1$ table; l-g/r: $N = 4$ tables; o/y: $N = 4$ tables). Although the foraging ranges of males -w, l-g/r and o/y were very similar, they differed noticeably from each of the areas used by o/-, r/- and y/b. Nevertheless, the foraging areas of all six target males overlapped to some extent. The nesting locations of each of the six pairs in Fig. 1, though, did not overlap and were at least 200 m apart.

We tracked five radiotagged crows for between 15 and 34 sessions in the latter half of 2004 (Table 2). We followed r/- for a total of 57.3 h, o/- for 90.4 h, r/b for 71.9 h, -w for 99.3 h and r/y for 51.7 h. Although we tracked the five birds for around 3 h per session, we only directly observed them for a much smaller amount of time. This was because the crows often moved locations and the forest conditions made it difficult to find them again quickly. Consistent with what we saw at feeding tables, we mostly observed the five radiotracked families foraging separately from other crows. Nevertheless, we also occasionally observed nonfamily crows in the vicinity of radiotracked birds and their family members. These associations were generally outside foraging activity, occurring both in the forest and garden patches during the day and at roost sites. For example, it was common to see many crows perching in

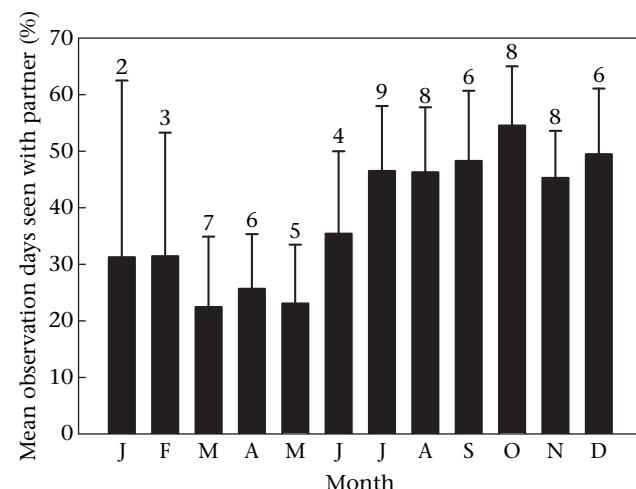


Figure 2. Association of target males with their partners: the mean percentage of observation days per month on which target males were seen with their partner at or away from feeding tables. The number of target males observed in each month is shown above the standard error bars.

dead trees in the gardens in the early mornings or when they were resting and preening themselves after rain. However, we never observed intimate physical contact such as grooming between members of different family groups. Nor did we see such contact between nonfamily birds when they were feeding from naturally occurring food sources such as papaya fruit hanging on trees.

Some juveniles of the target families continued to associate with their parents for at least 20 months post fledging (Fig. 3). The proportion of time that first-year juveniles spent with their parents decreased substantially during the next breeding season when they were around a year old. After the breeding season they were observed with their parents more frequently again, but less so than was usually the case in the first year.

Tolerance by Target Males at Feeding Tables

Each of the six target males in Fig. 1 visited 5–12 different feeding tables over the course of our study, and many tables were visited by more than one family. We videotaped 902 visits to feeding tables by the six males. We documented 137 cases from 91 visits when a target male was on the same table with a nonfamily crow (Table 5). Most of the nonfamily crows present were juveniles (exclusively so in 95 of the 137 cases). In 83 of the 137 cases, nonfamily crows fed when on the table with the target male. However, the feeding nonfamily birds were rarely close to the target males. For example, a nonfamily bird was sometimes foraging in the *Pandanus* sp. tree that we stood at the table while the target male was on the table. Nevertheless, it was not

Table 3
Persistence of pair bonds in six mated pairs

| Mated pair | First seen together | Last seen together | Known nesting years | Years known together |
|------------------------------|---------------------|--------------------|------------------------|----------------------|
| r/- and Pandora (family 1) | 13 Aug 2003 | 29 Nov 2004 | 2003, 2004 | 1.30 |
| l-g/r and Pandora (family 2) | 24 Jan 2005 | 29 Oct 2009 | 2005, 2007, 2008 | 4.76 |
| o/y and -go (family 3) | 25 Aug 2004 | 31 Oct 2006 | 2005, 2007 | 2.18 |
| o/- and -g (family 4) | 14 Sept 2003 | 11 Oct 2008 | 2003, 2004, 2005, 2007 | 5.08 |
| y/b and l-g/b (family 5) | 5 July 2004 | 29 Nov 2008 | 2005 | 4.41 |
| -w and r/b (family 6) | 14 Sept 2003 | 8 Nov 2005 | 2003, 2004 | 2.15 |
| r/y and b/g (family 9) | 19 Sept 2003 | 11 Jan 2005 | 2004, 2005 | 1.31 |

Other than family 1 where r/- was probably killed by a goshawk, the mated pairs were still together when we last saw them at the same location (column 3).

Table 4

The frequency with which target males were seen with partners and juveniles

| Target male | Total no. of observations | Target male alone | Partner present without juvenile(s) | Partner and juvenile(s) present | Juvenile(s) present without partner | Only nonfamily crows present | % Of total observations that partner was present |
|------------------|---------------------------|-------------------|-------------------------------------|---------------------------------|-------------------------------------|------------------------------|--|
| r/- (family 1) | 455 (89) | 114 (4) | 338 (85) | - (-) | - (-) | 3 (-) | 75.3 (95.5) |
| l-g/r (family 2) | 364 (254) | 136 (97) | 30 (21) | 77 (54) | 79 (53) | 42 (29) | 29.4 (29.5) |
| o/y (family 3) | 276 (139) | 75 (20) | 18 (2) | 3 (1) | 127 (104) | 53 (64) | 7.6 (2.2) |
| o/- (family 4) | 553 (152) | 239 (74) | 187 (20) | 1 (-) | 52 (42) | 74 (16) | 34.0 (13.2) |
| y/b (family 5) | 478 (224) | 165 (72) | 135 (32) | 46 (42) | 66 (61) | 66 (17) | 42.1 (33.0) |
| -/w (family 6) | 420 (72) | 82 (30) | 55 (5) | 107 (22) | 145 (13) | 31 (2) | 38.6 (37.5) |
| Total | 2546 (930) | 811 (297) | 763 (165) | 234 (119) | 469 (273) | 269 (128) | 39.2 (30.5) |

The observations are from late 2003 to the end of 2006, filmed or not, around and away from feeding tables. Most of the 2546 observations were at feeding table sites ($N = 2287$). The number of observations at feeding tables that were filmed is in parentheses. r/- was killed (probably by a goshawk) at his nest site before his juvenile y/wy fledged. The total number of observations is greater than the actual number because two or more target males were sometimes present at the same time.

uncommon for nonfamily juveniles to stop feeding and act submissively (e.g. lower head and/or move away) while the target male was present. Over the study period, the target males tended to share tables with more different nonfamily juveniles than different nonfamily adults. Most of the adults sharing tables with target males had foraging ranges that overlapped with those of the respective target male (15 of the 18 adult cases in the second-to-last column in Table 5). Although there were many banded adult crows around the study area excluding the nine target families, we rarely saw them on feeding tables with the target males. Therefore, it appeared that the target males were more tolerant of resident adults that they probably knew well.

The six target males visited tables alone at a significantly higher frequency in the breeding period (November–January) compared to other months of the year ($\chi^2_1 = 389.0$, $P < 0.0001$, $N = 232$; Fig. 4). Therefore, the males appeared to spend more time foraging alone over the nesting season, rather than just having a lower tolerance to nonfamily crows. Incubating partners and the lack of older offspring can only partly explain why the males foraged alone more often in the breeding season. This is because incubation only lasted around 18 days and only families 2 and 6 (target males l-g/r and -/w) nested when older offspring were still present.

Opportunities for Social Transmission at Tables

The target males infrequently shared feeding tables with nonfamily crows (Table 5), but it was possible that young juveniles

did so much more often. If so, it would increase the potential for horizontal transmission of tool information. However, seven juveniles in their first year rarely shared tables with nonfamily crows without other family members also being present (8.3% of 876 visits; Table 6). In contrast, they shared tables with family members (parents and/or siblings) on 50.3% of the 876 visits and were alone on 41.6% of the visits. In the juveniles' first year, at least one parent was present on 37.1% of their visits (Table 6). This percentage rose to 46.7% of visits in the months up to August of the first year when most parental feeding was observed. Siblings gy/l-g and oy/r, which both fledged in 2005, visited tables often ($N = 90$ visits) without their parents. Older siblings -/oy and y/wy were present with their younger siblings (o/o and y/or, respectively) on only 18 of the visits. We also looked at unfilmed visits to tables by the seven juveniles, as well as the filmed ones in Table 6, to see if they might be meeting other crows outside their parent's known foraging areas (see Fig. 1). Although some of the seven juveniles visited tables not known to be used by their father, only one first-year juvenile (o/o) was seen at a table outside the ringed area enclosing the tables on Fig. 1 that its father used (this occurred on two visits on the same day). Finally, the pattern of first-year juveniles rarely sharing feeding tables with nonfamily was generally consistent throughout the year (Fig. 5). Therefore, the potential for vertical transmission of tool skills via social learning was far greater than for horizontal transmission. Any vertical transmission of skills to first-year juveniles was also likely to be from parents rather than older siblings.

DISCUSSION

Our findings confirm the preliminary observations of Hunt (2000) and Kenward et al. (2004) suggesting that NC crows live mostly in small family units. We found that these family units were based on long-lasting pair bonds that were maintained year round. Furthermore, juvenile NC crows lived closely with their parents up to the following breeding season, and sometimes longer. However, we found no evidence that juveniles assisted with raising younger siblings.

Many authors have used group size as a measure of social intelligence and complexity (e.g. Dunbar 1998). However, group size alone appears to be a poor predictor for social complexity (Beauchamp & Fernández-Juricic 2004; Holekamp 2007). This seems to be particularly true for birds (Emery et al. 2007). Social network size, or the number of individuals having social relationships with each other (Wey et al. 2008), might therefore be a better measure of social complexity. The overlapping foraging areas of the NC crow families that we studied showed that the families did not defend exclusive territories (Fig. 1). For example, we observed the target families and other banded crows visiting and feeding in garden patches in loose groups. We found some evidence to suggest that paired males also recognized and tolerated resident adults in

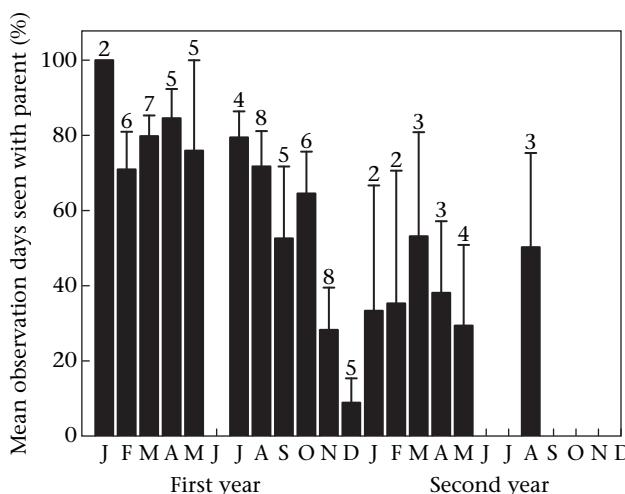


Figure 3. Observations of juveniles travelling with their parents: the mean percentage of bird observation days per month on which juveniles were seen with one or both parents. The number of juveniles observed in each month is shown above the standard error bars.

Table 5
Summary data when nonfamily crows shared feeding tables with target males

| Target male crow | No. of filmed visits to tables without/with nonfamily crow(s) | Cases when nonfamily crow(s) were present with/without other family members of the target male | | Cases when family members of the target male were present | | Age status of nonfamily crows | | Feeding at table ('family' was the target male and/ or other family members) | | Number of known individual nonfamily crows | | | | | | | |
|------------------|---|--|---------|--|-------|-------------------------------|----|--|----|--|-----|----|--------|----|------|--------|-----------|
| | | 1 bird | 2 birds | 3 birds | Total | P | J | P+J | A | J | A+J | ? | Family | NF | Both | Adults | Juveniles |
| r/- | 89/0 | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 | 0 | 0 |
| l-g/r | 224/30 | 5/27 | 2/4 | — | 7/31 | 1 | 6 | — | 3 | 31 | 4 | — | 2 | 25 | 2 | 5 | 5 |
| o/y | 125/14 | 8/6 | -3 | — | 8/9 | — | 8 | — | 3 | 11 | 1 | 2 | 4 | 2 | 7 | 1 | 9 |
| o/- | 140/12 | 1/8 | 3/2 | -2 | 4/12 | 2 | 2 | — | 2 | 8 | 3 | 3 | 4 | 2 | 8 | 4 | 6 |
| y/b | 18/28 | 3/10 | -6 | 21/44 | 9 | 10 | 2 | 6 | 45 | 9 | 5 | 14 | 4 | 34 | 10 | 14 | 14 |
| -w | 71/1 | 1/- | — | 1/- | — | 1 | — | 1 | — | — | — | — | — | 1 | 1 | 0 | 0 |
| | 839/91 | 33/70 | 8/19 | -8 | 41/96 | 12 | 27 | 2 | 15 | 95 | 17 | 10 | 26 | 11 | 72 | X=3.0 | X=5.7 |

Cases in columns 3–6 indicate when the focal target male was with a nonfamily crow(s) on a feeding table. The number of cases is often more than one per visit, but each case within a visit had a unique combination of nonfamily birds. The total number of filmed visits across the target males in column 2 (930) is greater than the actual total number (902) because two or more target males were sometimes present at the same time. The population of mated pairs in our study area between 2003 and 2006 was remarkable stable. Therefore, we did not adjust the numbers in the last two columns to account for differences in the number of years of data collection for each male. Also, there was no significant correlation between the total number of visits per target male and the total number of different nonfamily individuals (juveniles + adults) with whom they shared tables (Spearman correlation: $r_s = 0.58$, $N = 6$, $P = 0.23$). P = partner; J = juvenile; A = adult; ? = unknown; NF = nonfamily.

their area, who they probably observed on a daily basis. Nevertheless, each family at our study site appeared to interact with only a small proportion of the resident crow population. Data that we collected at feeding tables suggest that paired males at our study site had a relatively small social network size. The target males tolerated an average of around nine different nonfamily individuals on tables over the period of the study, as well as immediate family (Tables 4, 5). We never saw direct social interactions such as grooming or food sharing between family and nonfamily individuals, and only rarely witnessed aggressive encounters.

A social network would also include contacts based on agonistic interactions between individuals. This might have resulted in crows sometimes avoiding a feeding table because of intolerance to other bird's that were using it. Such cases are by their nature very difficult to assess and are not accounted for in this study. The reason why nonfamily juveniles were tolerated more than nonfamily adults might be that juveniles commonly display submissively when in close proximity to a nonfamily adult and are therefore less of a potential threat. Adult males might therefore tolerate submissive juveniles on the same feeding table even if they were unknown to them. The interactions between crows that we observed at feeding tables (e.g. submissive behaviours) may well be consistent with the existence of linear and stable hierarchies that have been documented in cooperatively breeding carrion crows, *Corvus corone*, which live in small family groups (Chiariati et al. 2010).

The likely social network size of NC crows is small compared to that of many other corvids. For example, rooks can nest within colonies of hundreds of pairs and may assemble in winter roosts of tens of thousands of individuals (Clayton & Emery 2007). Although they are unlikely to interact closely with all individuals of these huge groups, they probably have social interactions with many more individuals than NC crows do. The same applies to pinyon jays, which live in permanent flocks of 50–500 individuals (Balda & Bateman 1971; Marzluff & Balda 1989). Dealing with a large number of conspecifics does not seem to have been a daily problem for NC crows and thus may not have been a strong selection pressure on their cognitive evolution. However, the quality rather than the quantity of social relationships may also be important in the evolution of intelligence (Byrne & Whiten 1988; Emery et al. 2007). The social relationships of captive ravens were reported to be of a high quality only between immediate family (Fraser & Bugnyar 2010), as we found in NC crows. Therefore, high-quality social relationships within small family units might have contributed to the cognitive evolution of certain *Corvus* species such as ravens and NC crows.

The long period of parental care in NC crows is largely responsible for the high-quality relationships and distinguishes the species from most other corvids (dos Anjos et al. 2009). Some corvids, particularly those that breed communally such as pinyon jays and American crows, *Corvus brachyrhynchos*, allow their juveniles to remain within the parental foraging area for extended periods after fledging (Caffrey 1992; Langen 1999; Clayton & Emery 2007). The Mariana crow, *Corvus kubayari*, which lives on the small tropical island of Rota is also reported to tend its juveniles well into their second year (Morton et al. 1999). However, Morton et al. (1999) did not explicitly state how long parental feeding continued. Extended parental care may be more prevalent in tropical and temperate regions, possibly associated to some extent with generally lower but more stable food resources (Russell 2000). One explanation for the extended care of juveniles is that it enables inexperienced birds to learn complex or time consuming foraging techniques in niches where food is not easily accessible (Heinsohn 1991). At the end of their first year, juvenile NC crows have still not reached adult proficiency (e.g. adult speed) in their complex foraging techniques that involve tool use (Holzhaider et al. 2010).

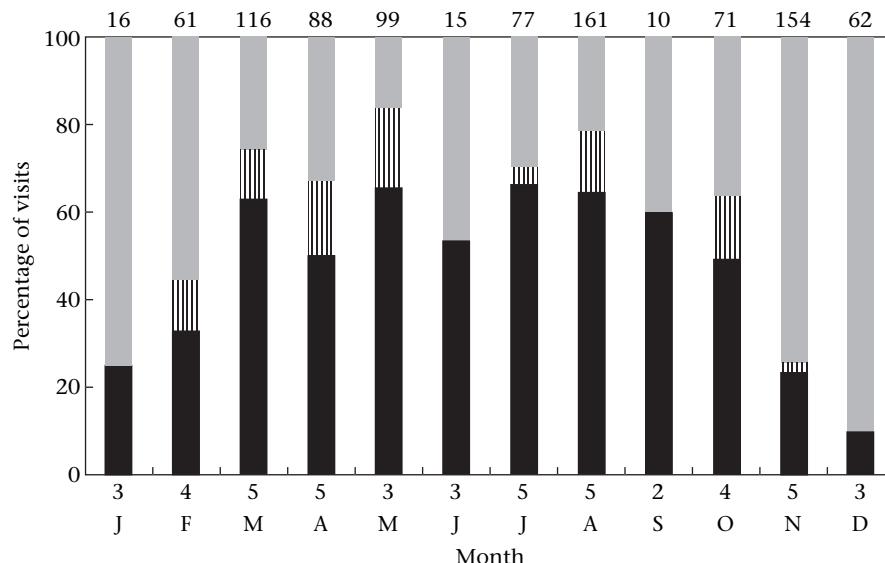


Figure 4. The frequency with which six target males visited feeding tables in each month. The total number of visits per month is shown above the bars (this is greater than the actual number when two or more of the six males were present at the same time). The number of target males observed in each month is shown below the bars. Grey: visits alone; black: with only immediate family; vertical bars: with nonfamily (family may also be present).

The low frequency with which NC crow parents feed second-year offspring indicates that they are nutritiously independent long before the parents stop feeding them altogether. However, juvenile begging and subsequent feeding by a parent might maintain the juvenile–parent relationship and thus allow juveniles to continue living in close association with their parents. Living in such an environment of reduced intraspecific competition and predation threat might assist juveniles in perfecting their foraging skills. That juveniles might delay dispersal to profit from a ‘safe haven’ provided by their parents has been suggested for other bird species such as the Siberian jay, *Perisoreus infaustus* (Ekman & Griesser 2002).

NC crows stand out from other corvids because of their tool use in the wild. According to the technical intelligence hypothesis, the demands of extractive foraging might provide an explanation for their considerable cognitive abilities and high degree of encephalization. Sterelny (2007) proposed a ‘social intelligence–ecological complexity hybrid’, arguing that social and technological competence became coupled in early hominins. Through niche construction (Odling-Smeek et al. 2003; Sterelny 2003) they changed their environment so it provided new challenges and opportunities to develop technology for future generations. Two aspects of NC crows’ lifestyle are consistent with this idea. The first is that high-quality social relationships appear to be restricted to immediate family. The second is that parents facilitate the

acquisition of their juveniles’ tool skills by strongly scaffolding their learning environment over an extended period of time (Holzhaider et al. 2010). Thus the social organization of NC crows on Maré is potentially suitable for the evolution of the generational transmission of tool skills because it promotes vertical transmission while minimizing the opportunity for horizontal transmission. Vertical transmission is considered to be crucial for the faithful spread of technological innovations (Sterelny 2006).

In general, close proximity between individuals increases the likelihood that one can observe details of others’ behaviours (Coussi-Corbel & Fraga 1995). van Schaik et al. (1999) claimed that strong mutual tolerance between individuals was a key factor in the evolution of technology among hominids, tied to a lifestyle involving food sharing and tool-based processing of food. NC crows in our study were highly tolerant towards family members, with whom they readily shared feeding tables. Juveniles in their first year predominantly visited tables with their parents rather than older siblings and/or nonfamily crows (Table 6, Fig. 4). Young juveniles can also watch their parents’ tool use and tool manufacture from close proximity and use their discarded tools, and are fed much of the food that parents extract at feeding tables (Holzhaider et al. 2010). Juveniles therefore have ample opportunity to obtain tool skills vertically from their parents. However, they also shared tables with nonfamily crows (Table 6, Fig. 4), and the target males appeared to be generally more tolerant of nonfamily juveniles than

Table 6

The frequency that first-year juveniles associated with family and nonfamily on feeding tables

| | Juvenile | First year | Number of filmed visits | Visits alone | Only with parents and/or siblings | With both family and nonfamily | Only with nonfamily |
|----------|----------|------------|-------------------------|--------------|-----------------------------------|--------------------------------|---------------------|
| Family 2 | y/wy | 2005 | 135 | 57 | 71 (71) | - (-) | 7 |
| | y/or | 2006 | 80 | 27 | 43 (39) | 6 (6) | 4 |
| Family 3 | oy/r | 2006 | 304 | 142 | 105 (63) | 20 (13) | 37 |
| | gy/l-g | 2006 | 196 | 63 | 108 (60) | 15 (8) | 10 |
| Family 4 | bo/- | 2006 | 71 | 29 | 33 (33) | 2 (2) | 7 |
| Family 6 | -/oy | 2004 | 14 | 9 | 3 (3) | 1 (1) | 1 |
| | o/o | 2005 | 76 | 37 | 31 (25) | 1 (1) | 7 |
| Total | | | 876 | 364 | 394 (294) | 45 (31) | 73 |

The total number of visits ($N = 876$) is greater than the actual number because two or more of the juveniles were sometimes present at the same time. The number of visits when at least one parent was present is in parentheses.

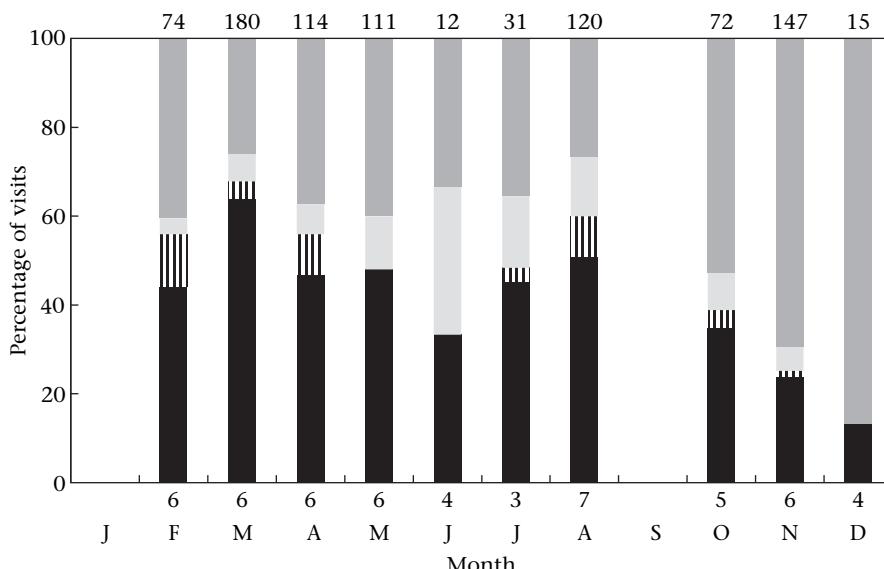


Figure 5. The opportunity for social learning by seven first-year juveniles. The total number of visits per month is shown above the bars (this is greater than the actual number when two or more of the seven juveniles were present at the same time). The number of juveniles observed in each month is shown below the bars. Dark grey: visits alone; black: with only immediate family; vertical bars: with both family and nonfamily; light grey: with only nonfamily.

of adults other than their partners (Table 5). Similarly, adult chimpanzees, *Pan troglodytes*, are highly tolerant of juveniles even if they are not their own offspring, which increases juveniles' opportunities to observe tool use by experienced individuals (Matsuzawa et al. 2001). In contrast, the opportunity for young crows to learn tool skills from their immediate family (vertical transmission) is much greater than from nonfamily (horizontal transmission). Horizontal transmission therefore appears unlikely to play a major role in the acquisition of tool skills by juveniles. An important implication of the dependence on vertical transmission is that the spread of tool use in NC crows would have occurred over a relatively long period of time by tool-using birds replacing those that did not use tools.

In summary, much of the lifestyle of NC crows is similar to that of other corvids. However, with a small social network size they are one of the less social Corvidae. Their core social unit is immediate family, with whom they travel year round. Parents are highly tolerant of their juveniles and can feed them well into their second year of life. NC crows' close and long-lasting relationships with partners and juveniles is also consistent with the hypothesis that from a cognitive point of view, the quality of relationships in birds is more important than the quantity (Emery et al. 2007). Small social networks, extended parental care and high-quality social relationships restricted to immediate family are possible social factors associated with NC crows' impressive tool skills and the evolution of their cognitive abilities. The social system of NC crows thus provides important prerequisites for the cumulative technological evolution of the pandanus tool designs.

Acknowledgments

We thank William Wadrobert for kindly allowing us to work on his family's land in Wabao District, Maré, and the Province des îles Loyauté for permission to work on Maré. Roland Rehm assisted with data collection and maintaining tracks and tables in the forest. We thank two referees and Thomas Bugnyar for comments that much improved the paper. This research was funded by a grant from the New Zealand Marsden Fund (R.D.G. and G.R.H.).

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