# Morphology and sexual dimorphism of the New Caledonian Crow *Corvus moneduloides*, with notes on its behaviour and ecology

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New Caledonian Crows *Corvus moneduloides* are known to be extraordinary tool makers and users, but little is known of other aspects of their biology. Here, we report recent field observations of their behaviour and ecology, along with measurements of 19 morphological traits and two flight performance parameters taken from 22 captured Crows. These measurements showed that the Crows were sexually dimorphic in size (the males were larger) but not in shape. We also found that the crows lived in mixed-sex groups, and we observed juvenile-type begging behaviour and feeding by regurgitation, which supports the hypothesis that these may be family groups.

The New Caledonian Crow *Corvus moneduloides* is endemic to the semitropical Grande Terre island of New Caledonia in the South Pacific. This species has recently become a focus of interest because of its complex tool-oriented behaviour, which includes species-wide manufacture of a diverse range of tool types (Hunt & Gray 2002), laterality in tool manufacture (Hunt 2000a, Hunt *et al.* 2001) and use (Rutledge & Hunt 2004, Weir *et al.* in press), hook manufacture from natural substances and from novel material (Hunt 1996, Weir *et al.* 2002, Hunt & Gray 2003a), flexibility of tool selection (Chappell & Kacelnik 2002) and shaping of material to a rule system (Hunt 2000a, Hunt & Gray 2003b). There is also strong indirect evidence for cumulative change in tool design, mediated by social transmission (Hunt & Gray 2003c). Although some of these behaviours are rare or unknown in non-human animals, very little is known of other aspects of the Crows' biology. In this context there is a great need to learn more, and the possible existence of socially transmitted cumulative technology means that a better understanding of their social dynamics is essential.

The main thrust of our research programme is to study cognitive aspects of the Crows' tool use. To this end, in 2002 we spent 6 weeks observing Crows in New Caledonia with the main intention of trapping a sample for captive study. This gave us an opportunity to make our own observations of their wild behaviour, and also to learn more about the composition of their social groups, because we were able to determine the sex of the captured individuals *post facto* and to observe their interactions over a long period at close quarters in captivity. The second opportunity presented to us by captive birds is the ability to make detailed morphological measurements, which enable both the identification of any sexual dimorphism and also comparisons with other species.

We begin by summarizing current ecological and morphological knowledge, and then present the methods and results of our observations, captures and morphological measurements.

## CURRENT KNOWLEDGE OF NEW CALEDONIAN CROW ECOLOGY AND MORPHOLOGY

The New Caledonian Crow's diet includes insects and their larvae, snails, nuts, fruit, seeds, flowers, and other birds' eggs (Layard & Layard 1882, Hannecart & Letocart 1980). Their tool use seems exclusively directed at obtaining insects and other invertebrates, and their techniques can be divided into two classes: those for obtaining large cerambycid larvae, which bore deep into wood, and those for obtaining small invertebrates from under bark and in other crevices (Hunt & Gray 2002). The proportion of their diet

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typically made up of invertebrates obtained by tool use is unknown. Many corvids engage in other behaviours, which may be cognitively complex, such as food caching and the breaking of snails or nuts by dropping, and both these behaviours have been documented in the New Caledonian Crow (Hunt 2000b, Hunt *et al.* 2002).

New Caledonian Crows are common throughout the range of forest types found on Grande Terre (Hunt 2000a, personal observations by B.K., A.W. and C. Burn (field assistant)) and are also found in the Niaouli savannah (Hannecart & Letocart 1980) and in agricultural areas (Vuilleumier & Gochfeld 1976, our pers. obs.). The Crows usually occur in groups ranging in size from pairs up to 30 birds, though most often the groups are small, and it has been suggested that the larger groups are temporary conglomerations of multiple small groups (Hunt 2000b). It has also been assumed that these are family groups; certainly, nutritionally independent juveniles have been seen closely associating with adults (Hunt 2000b). There is some evidence that group size varies across areas (Hunt 2000a). The literature does not agree precisely on nesting period, although the most authoritative source (Hannecart & Letocart 1980) gives it as October–January, and states that clutch size is one or two.

Their appearance is that of a 'typical' crow (*sensu* Goodwin & Gillmor 1986), except for the unusually shaped bill, particularly the maxilla, which has almost no downwards curve. Although the weights of 22 dead crows have been reported (mean 275.4 g (*n* = 22), males 289.3 g (*n* = 7), females 275.4 g (*n* = 13)), no statistics were calculated in the above study to examine the significance of the apparent sexual dimorphism in weight (Ross 1988).

## METHODS

### Field observations and capture

During July and August 2002, we observed and caught Crows from three trap sites in the west of New Caledonia. Two sites were approximately 1 km apart in the Ouatchoué river valley near Boulouparis (21°53.200′S, 165°59.076′E, elevation 20 m; and 21°52.646′S, 165°59.513′E, elevation 20 m) and the third was approximately 40 km away in the Moindou river valley near Tendéa (21°38.054′S, 165°43.830′E, elevation 240 m). The two areas had different habitats: the Boulouparis sites were in low-lying farmland with more open areas, and the Tendéa site was less cultivated, with more forest and a different composi-

tion of tree species owing to the altitudinal difference. We baited each area with meat and carried out observations for several days until groups of Crows were feeding there regularly. We used a whoosh net (supplied by P. Reid, pete@whoosh.fslife.co.uk), which enabled us to catch groups of co-feeding Crows. The net was only released if we were as certain as we could be that any juveniles accompanying the group were inside the catching area, to minimize the possibility of separating them from their parents.

The captured Crows were housed in aviaries at Park Forestier, Nouméa, New Caledonia. Blood samples were taken for sex determination by genetic analysis (see Appendix 1), before the birds were shipped by air to the UK.

## Morphology

### Subjects

In total, 21 of the captured Crows (13 males and eight females) were sent to Oxford, UK, where they joined one female Crow caught previously in March 2001 on the coast at Yaté (approximately 22°11′S, 166°57′E, at sea-level), making our sample 22 birds. At the time of measurement, the Crows were housed in two groups, one of ten and one of 12 individuals, each with indoor and outdoor accommodation. Each group consisted of Crows from only one area (except for the single female from Yaté, which was housed with the Tendéa birds).

### Measurements

On 6 May 2003 the birds in one group were caught and measured, with the remaining group measured on 9 May. During each session, three birds from the other group (the first three birds that we could catch) were also measured as replicates, to estimate our measurement error. The Crows were deprived of food but not water 15 h before measurement to reduce weight variation due to gut contents (they are usually fed *ad libitum*). Of the 22 Crows, 16 had also been weighed on the day of capture in the wild.

We are not aware of a method to determine the age of these Crows, but if the latest nesting is January they are all likely to have been at least 16 months old at the time of measurement. We measured 17 variables from each of the 22 Crows, and took wing profiles from 13. The wing profiles were used to calculate morphological flight parameters (total wing area, wing span, aspect ratio and wing loading), giving a total of 21 variables. For details of the measurements, see Table 2 and Appendix 2.

*Statistical analyses*

To analyse variation between the sexes it was first necessary to test that capture site was not responsible for variation, because the proportion of males from Tendéa was higher than that from Boulouparis. For three response variables (weight, tarsus length and head width), we calculated a general linear model (GLM) with sex and site as fixed factors (e.g. Grafen & Hails 2002) (all statistical calculations were performed with SPSS v. 11.5.0, from SPSS Inc). Because of the close proximity of the two sites at Boulouparis, we considered them to be one site for this analysis, and we excluded the single Crow caught at Yaté; there were thus two sites analysed. It is standard for sex to be a fixed factor in a GLM. Because site is included as a fixed factor it is not valid to make general conclusions from this model regarding Crows caught from other sites. Unfortunately, we could not include site as a random factor in a general linear mixed model (GLMM) because, with only two female Crows from Tendéa, our power would have been too low to draw any conclusions.

To quantify any sexual dimorphism present, we calculated a mean for each sex for each of the morphological variables, and applied *t*-tests to check for significant differences. Because we were testing 21 variables, we applied a Bonferroni correction for multiple *P*-values (e.g. Sokal & Rohlf 1995) to obtain a threshold of statistical significance of 0.002. We were also interested in whether there might be sexual dimorphism in shape as well as size. To examine this, we calculated ratios between each pair of the following variables, which we considered to be most biologically meaningful: bill depth at base, gonys length, head width, head length excluding bill and tarsus length. We then applied *t*-tests on the ten ratios obtained for each individual to check for significant sex differences. Bonferroni correction gave a threshold of statistical significance of 0.005 for these tests.

We also used discriminant function analysis (DFA) to obtain a mathematical function that would allow us to predict the sex of a bird (e.g. Renner *et al.* 1998). We only included variables for which we had obtained a valid measurement for every bird, to maximize our data set. We used a forward stepwise method in which each variable is introduced into the function, in order of maximum discriminatory power (measured by the overall Wilks' lambda), until there is no variable left with an *F*-value at least as significant as 0.05. We also required a function that was not dependent on weight (which is more prone to vary due to factors such as season or condition), so we also performed a DFA excluding weight.

Discriminant functions are most reliable when they can be verified by testing with data that were not used to generate the functions. However, our limited sample size meant that we needed to use all available data, so we performed a jack-knife analysis (Sokal & Rohlf 1995). To test for normality, each variable distribution (including the calculated ratios) was compared, using a Kolmogorov–Smirnov test, with a normal distribution generated mathematically with the same parameters (Sokal & Rohlf 1995). Because our GLMs and *t*-tests compared the effects of sex and site, we performed separate tests for normality with the variable distributions divided by those factors. These tests indicated that none of the distributions deviated significantly from normality. The data also satisfied the other assumptions necessary for DFA: there was no significant difference between the covariance matrices for the sexes (Box's $M = 25.3$, $P = 0.27$), and within-sex correlation coefficients were low (maximum 0.505), showing that there was little co-linearity.

## RESULTS

### Observation in the field and capture

At Tendéa we had an excellent vantage point from which we could see for hundreds of metres both across and up and down the valley. The Crows often flew above the canopy across the valley, allowing us to see that there were often several separate groups in an area of roughly 1 km². The groups appeared to some extent fluid, with individuals joining or leaving groups and flying off in different directions. In both areas we saw solitary birds, but groups were more usual. These varied in size from pairs up to eight, with median and mode both of three, and mean of 3.8 (se = ± 0.18, *n* = 100). However, these statistics should be regarded with caution, because: (a) group fluidity and dense vegetation hindered counting, (b) we did not record group size every time we saw Crows and (c) most of the counts were made at the three trap sites so individuals and groups will have been counted more than once.

When there were temporary large groups of Crows, they were often much noisier than usual, producing a very loud high pitched *wak–wak* vocalization (Goodwin & Gillmor 1986). (Given the acoustic properties of this call and the fact that it is most commonly made when birds are out of visual contact with one another, we believe it may generally serve as a contact call.) Carrion seemed to be a regular component of the Crows' diet as there are many pig and

deer carcasses in the forest. For this reason our extra provision of food was probably not creating artificially high concentrations of Crows, and we saw similar concentrations of Crows at sites that we had not baited.

We observed some individuals begging, with a characteristic vocalization, wing-holding and gaping, and they were occasionally fed by regurgitation. Bouts of begging behaviour were occasionally prolonged and insistent. In these instances the target of the begging was often forced to move away and was tenaciously followed from perch to perch. We know that some of the Crows showing begging behaviour were nutritionally independent, as we observed them feeding themselves from our bait. However, if nesting occurs until January (Hannecart & Letocart 1980), these begging Crows were at least 7 months old when we made our latest observation of begging behaviour (21 August).

We recorded a number of aggressive interactions between Crows, all of which occurred around the bait. These interactions were rarely serious and usually seemed to be dominance interactions within a group, in which an individual was forcibly displaced from its feeding position, rather than territorial interactions. Sometimes solitary individuals waited in trees above the bait until a feeding group had left, and then fed themselves. These individuals were much more vigilant than Crows in groups. Mobbing of raptors (some identified as Whistling Kites *Haliastur sphenurus*) was also common: raptors were frequently attracted to our bait, but the Crows invariably displaced them from the meat. Some of the largest group sizes we saw occurred when the Crows were defending carrion from raptors, and it seemed likely that different groups were coming together to mob. There was much *wak–wak* vocalization during these periods.

Table 1 shows the results of trapping and sexing. The group sizes shown are not representative of the average group size we observed, as we were more likely to fire the net when there were larger groups. In total we caught 26 Crows in eight groups, comprising 15 males and 11 females. This is not a significant deviation from a 50 : 50 ratio ($\chi^2_1 = 0.727$, $P = 0.394$). Every group captured was mixed-sex, although there were two captures of solitary birds.

## Morphology

### Error and validity of measurements

Some of the Crows had damaged plumage at the time of measurement. Three had broken primary

**Table 1.** Date of capture, site and sex composition of trapped groups of New Caledonian Crows.

| Date | Site | No. captured[a] | N males | N females |
|---|---|---|---|---|
| 28/7/02 | Boulouparis 1 | 1 (3) [3] | 1 | 0 |
| 29/7/02 | Boulouparis 1 | 4 (0) [2] | 3 | 1 |
| 29/7/02 | Boulouparis 1 | 4 (1) [2] | 1 | 3 |
| 1/8/02 | Boulouparis 2 | 5 (0) [3] | 2 | 3 |
| 1/8/02 | Boulouparis 2 | 2 (1) [0] | 1 | 1 |
| 1/8/02 | Boulouparis 2 | 1 (0) [0] | 0 | 1 |
| 22/8/02 | Tendéa | 4 (0) [0] | 3 | 1 |
| 30/8/02 | Tendéa | 5 (1) [0] | 4 | 1 |

[a]Numbers in parentheses indicate Crows that were feeding on the bait but escaped the net. Numbers in square brackets indicate Crows that were seen in nearby trees and might have been members of the group that was caught.

remiges, and three had broken central rectrices. Wing and tail measurements from these birds were therefore excluded from the analysis. As noted earlier, we were unable to age birds, so differences in plumage stages could be a source of error. Some individuals had moulted in captivity, but all of the longest primary remiges and central retrices were fully regrown. Although it is normal in wild birds for the tip of the maxilla to project slightly over that of the mandible, in 11 birds the maxilla projected more than 1.5 mm, which we considered to be an excessive overgrowth due to captive housing. For these birds we therefore excluded the following maxilla measurements: culmen length, culmen length to nostril and head length. Head length excluding bill was still valid for those birds despite being calculated from head length including bill, because the culmen length had been subtracted.

Our measurement error, determined by comparison between the measurements for the six birds that were measured twice, was in general very low (Table 2). For all measurements made with callipers, the greatest error was 1.8 mm (for a tarsus length measurement), and the greatest mean error was 0.8 mm (again for tarsus length), which is 1.5% of the mean variable value. Maximum error for the body girth measurements, which we had suspected might be inaccurate, was 7 mm, which is 2.5% of the mean variable value.

The Crows gained weight significantly during their period in captivity (paired samples *t*-test, $n = 16$, $t_{15} = 5.829$, $P < 0.001$). During the 9–10 months from capture, their weight increase averaged 32 g and there was no sex difference in weight gain (*t*-test, *n* males = 9, *n* females = 7, $t_{14} = -1.274$, $P = 0.224$). However, the procedure for weighing the birds in
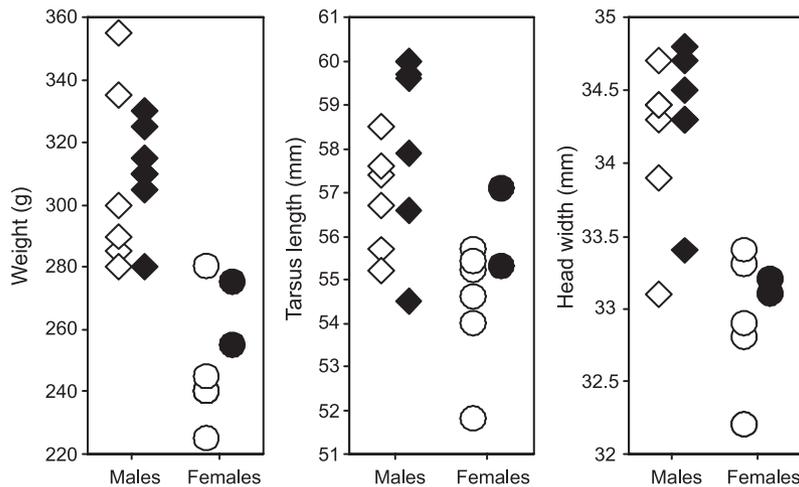
**Figure 1.** Morphometrics of New Caledonian Crows by sex. Filled symbols represent birds from Tendéa, empty symbols those from Boulouparis.

the field was different and possibly more subject to error. The weight gain in captivity could have been due to increased food provisioning or to juvenile growth, but because the proportional gain in weight was not correlated with weight at capture, the first explanation seems more likely (linear regression, $n = 16$, $F_{15} = 3.609$, ns). The fact that weight changed in captivity raises the possibility that other measurements could also have changed. This cannot be ruled out, as weight was the only measurement taken at the time of capture, but measurements that depend mainly on skeletal size (such as tarsus length) are unlikely to have changed in adult birds over the course of 8 months.

### Effects of site and sex
In all the variables for which we calculated GLMs (weight, tarsus length and head width), sex explained a significant amount of variation, but neither site nor the interaction between site and sex explained any significant variation (Fig. 1) (weight: by sex $F_{1,17} = 25.149$, $P < 0.001$, by site $F_{1,17} = 1.157$, $P = 0.297$, by interaction $F_{1,17} = 0.605$, $P = 0.447$; tarsus length: by sex $F_{1,17} = 7.686$, $P = 0.013$, by site $F_{1,17} = 3.907$, $P = 0.065$, by interaction $F_{1,17} = 0.028$, $P = 0.870$; head width: by sex $F_{1,17} = 26.084$, $P < 0.001$, by site $F_{1,17} = 1.229$, $P = 0.283$, by interaction $F_{1,17} = 0.099$, $P = 0.757$). The *t*-tests that test for sexual dimorphism are therefore valid despite the difference in proportions of the sexes from the different sites.

### Quantifying sexual dimorphism
For all the size variables measured, the means for males were greater than those for females, significantly so

for ten of 19 variables (Table 2). A lack of power and conservatism of the Bonferroni correction probably accounted for the non-significance of the differences in the remaining variables. The absolute differences were not great – the linear measurements for the males were on average 6.4% longer, and the males were 24% heavier. The differences were, however, quite reliable – only one female was as heavy as the lightest male (Fig. 1). The dimorphism was unlikely to have been a result of captivity conditions, because the males were also significantly heavier on the day of capture (independent samples *t*-test, $n = 16$, $t_{14} = -3.383$, $P < 0.01$). The sexes did not differ significantly in any of the ratios calculated, indicating that the dimorphism is primarily in size rather than in shape. Neither did the sexes differ in flight morphology variables, although as we only had four wing profiles for females, the power of this comparison was low.

The variables entered into the first DFA were gonys length, bill depth at base, beak height at nostrils, beak width at base, bill width at nostrils, head width, head length excluding bill, tarsus length, body girth and weight. The resulting discriminant function was:

$$D = 0.378 * \text{tarsus length} + 1.198 * \text{head width} + 1.888 * \text{bill depth at nostrils} - 1.479 * \text{bill width at nostrils} + 0.043 * \text{weight} - 87.073.$$

*D* is greater than zero for males and less than zero for females. This function correctly classified all 22 individuals. The jack-knife analysis produced functions that in every case correctly classified the individual omitted. The discriminant function obtained when weight was removed from the analysis was:

**Table 2.** Morphometrics of New Caledonian Crows trapped in 2002. Error estimates are based on six replicate measurements. All measurements were made using standard methods or as explained in the table footnotes.

| Variable | n | All Mean (±sd) | n | Female Mean (±sd) | n | Male Mean (±sd) | Sex comparison t-test t | df | P | Error Mean | Max. | Mean as % of mean variable value |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Culmen length[ai] (mm) | 11 | 45.0 ± 2.7 | 4 | 42.2 ± 1.3 | 7 | 46.6 ± 1.6 | −4.686 | 9 | 0.001* | 0.3 | 0.9 | 0.6 |
| Culmen length to nostril[bi] (mm) | 11 | 30.2 ± 1.7 | 4 | 28.5 ± 0.4 | 7 | 31.2 ± 1.3 | −4.064 | 9 | 0.003 | 0.3 | 0.7 | 0.9 |
| Gonys length[ci] (mm) | 22 | 26.5 ± 1.4 | 9 | 25.5 ± 0.6 | 13 | 27.2 ± 1.3 | −3.526 | 20 | 0.002* | 0.3 | 0.6 | 1.1 |
| Bill depth at base[ci] (mm) | 22 | 20.9 ± 1.1 | 9 | 20.0 ± 0.6 | 13 | 21.4 ± 1.0 | −3.743 | 20 | 0.001* | 0.6 | 1.3 | 2.9 |
| Bill depth at nostrils[ci] (mm) | 22 | 18.3 ± 1.0 | 9 | 17.4 ± 0.4 | 13 | 18.9 ± 0.8 | −5.093 | 20 | < 0.001* | 0.5 | 1.4 | 2.5 |
| Bill width at base[ci] (mm) | 22 | 20.9 ± 1.1 | 9 | 19.3 ± 0.8 | 13 | 19.9 ± 0.6 | −1.825 | 20 | 0.083 | 0.3 | 0.5 | 1.4 |
| Bill width at nostrils[ci] (mm) | 22 | 18.3 ± 1.0 | 9 | 14.2 ± 0.9 | 13 | 14.7 ± 0.6 | −1.445 | 20 | 0.164 | 0.5 | 1.2 | 3.7 |
| Head width[ci] (mm) | 22 | 33.7 ± 0.8 | 9 | 32.9 ± 0.4 | 13 | 34.2 ± 0.5 | −6.325 | 20 | < 0.001* | 0.4 | 1.2 | 1.1 |
| Head length including bill[di] (mm) | 11 | 83.5 ± 2.8 | 4 | 80.1 ± 0.4 | 7 | 85.4 ± 1.1 | −9.202 | 9 | < 0.001* | 0.2 | 0.5 | 0.2 |
| Head length excluding bill[e] (mm) | 22 | 38.4 ± 1.3 | 9 | 37.8 ± 1.1 | 13 | 38.8 ± 1.2 | −1.832 | 20 | 0.082 | 0.6 | 1.4 | 1.5 |
| Tarsus length[fi] (mm) | 22 | 56.5 ± 2.2 | 9 | 54.9 ± 1.4 | 13 | 57.6 ± 1.9 | −3.648 | 20 | 0.002* | 0.8 | 1.8 | 1.5 |
| Tarsus height[ij] (mm) | 22 | 6.5 ± 0.4 | 9 | 6.2 ± 0.4 | 13 | 6.7 ± 0.3 | −3.402 | 20 | 0.003 | 0.2 | 0.5 | 2.6 |
| Tarsus width[ik] (mm) | 22 | 5.0 ± 0.4 | 9 | 4.8 ± 0.3 | 13 | 5.1 ± 0.4 | −1.749 | 20 | 0.096 | 0.4 | 0.8 | 8.7 |
| Body girth[cl] (cm) | 22 | 18.8 ± 1.1 | 9 | 17.8 ± 0.7 | 13 | 19.5 ± 0.7 | −5.257 | 20 | < 0.001* | 0.5 | 0.7 | 2.5 |
| Weight[m] (g) | 22 | 284.8 ± 36.4 | 9 | 249.4 ± 17.8 | 13 | 309.2 ± 22.8 | −6.586 | 20 | < 0.001* | 6.7 | 15 | 2.3 |
| Wing length[gn] (cm) | 19 | 26.4 ± 1.1 | 6 | 25.2 ± 0.5 | 13 | 26.9 ± 0.8 | −4.481 | 17 | < 0.001* | 0.1 | 0.2 | 0.2 |
| Tail length[hn] (cm) | 19 | 16.8 ± 0.9 | 8 | 16.1 ± 0.6 | 11 | 17.3 ± 0.7 | −3.751 | 17 | 0.002 | 0.1 | 0.2 | 0.7 |
| Total wing area[o] (cm$^2$) | 13 | 1056.7 ± 111.8 | 4 | 950.7 ± 116.3 | 9 | 1103.8 ± 74.5 | −2.898 | 11 | 0.015 | – | – | – |
| Wing span[o] (cm) | 13 | 71.4 ± 5.3 | 4 | 66.8 ± 6.3 | 9 | 73.4 ± 3.4 | −2.476 | 11 | 0.031 | – | – | – |
| Aspect ratio[o] | 13 | 4.83 ± 0.30 | 4 | 4.71 ± 0.36 | 9 | 4.89 ± 0.27 | −1.033 | 11 | 0.324 | – | – | – |
| Wing loading[o] (g/cm$^2$) | 13 | 0.275 ± 0.031 | 4 | 0.257 ± 0.032 | 9 | 0.283 ± 0.028 | −1.502 | 11 | 0.161 | – | – | – |

[a]Length of exposed culmen as in Baldwin *et al.* (1931), except we define the base of the culmen as where it meets the skin rather than the feathers because this measurement seems more repeatable.
[b]Position of nostril in maxilla from tip of bill as in Baldwin *et al.* (1931).
[c]As in Baldwin *et al.* (1931).
[d]Measured from the tip of the bill to the most posterior part of the head.
[e]Calculated by subtracting length of culmen from length of head including bill.
[f]With foot bent, the distance from the intertarsal joint to the last undivided leg scute.
[g]Maximum wing length when fully flattened and stretched.
[h]Length of fully flattened and stretched central rectrices, measured underneath.
[i]Measured with digital callipers to the nearest 0.1 mm.
[j]Major diameter close to foot.
[k]Minor diameter close to foot.
[l]Measured with a tailor's tape measure to the nearest 1 mm.
[m]Measured with a spring balance to the nearest 5 g.
[n]Measured with a ruler to the nearest 1 mm.
[o]Calculated as in Appendix 2.
*Significant difference between sexes of *P* = 0.002.

$D = 1.862 *$ head width $+ 1.168 *$ bill depth at
   nostrils $- 84.134$.

This function also classified all 22 individuals correctly. However, the jack-knife analysis without weight misclassified two males as females, giving a 90.9% success rate.

## DISCUSSION

### Sexual size dimorphism

Many hypotheses have been proposed to explain sexual size dimorphism in birds (e.g. Blondel *et al.* 2002). Our knowledge of New Caledonian Crow ecology does not allow us to rule many of them out. One explanation that does seem unlikely is niche differentiation to reduce intrasexual competition (e.g. Shaffer *et al.* 2001), because we know that the Crows forage in mixed-sex groups (we caught Crows in mixed-sex groups while they were foraging). In captivity at least, observations indicate that both sexes are similarly prepared to use tools to obtain wood-boring insects, which are otherwise difficult to obtain, although we do not yet know whether the sexes differ in the size or kind of tools they make and use, or in the sort of prey they seek. We have reported here that we found no shape dimorphism in New Caledonian Crows. Had we found such a difference, it might have been an indicator of niche differentiation resulting from the different selection pressures on individuals experiencing different environments. For example, Wandering Albatrosses *Diomedea exulans* sexes may differ in flight morphology because they forage in different ocean areas (Shaffer *et al.* 2001).

Other proposed hypotheses relate to sexual selection (e.g. Andersson 1994). One suggests that strong intermale competition for females promotes an increase in body size in males. This hypothesis predicts that in species or populations with greater male–male competition, sexual size dimorphism will be greater. Another hypothesis suggests that the necessity for territorial defence may promote sexual size dimorphism, especially if there is a division of roles within the pair. We know too little about the reproductive behaviour of the Crows to comment on the applicability of these hypotheses.

The DFA distinguished effectively between the sexes. Genetic analysis, although certainly more reliable, is time consuming and expensive, so our functions could have applicability in the field. However,

it should be noted that body size can vary within a species between different populations, and we have generated the functions using data from only two sites. We were able to use a GLM to confirm that the dimorphism we discovered was not due to variation between sites. However, because of our small sample size we were not able to use a more powerful GLMM, which would allow us to generalize our results to other areas. In addition, because our Crows gained weight in captivity, we would not advocate using our functions to sex Crows from other areas – although it is likely that the larger of a breeding pair would be the male.

Weight gain in captivity could be due to increased availability of food, and/or to the possibility that we caught juveniles that were not then fully grown. Ross's (1988) wild birds were 10 g lighter than ours in captivity, which supports the hypothesis that the birds gained weight, but does not indicate the magnitude of the effect.

### Flight morphology

Rayner (1988) has plotted regression lines of flight morphology parameters for a very large number of bird species. Including our results as points on his figures 12 and 13 reveals that in relation to body mass, the wings of New Caledonian Crows are of average length but with larger area than expected, meaning they have low wing loading. The low wing loading is explained by the wings being broader rather than longer. This is appropriate for a woodland bird that routinely navigates its way past branches and other obstacles. There is no evidence that the sexes differ in flight performance. It would be difficult to draw further conclusions from these parameters without the opportunity to compare these data with other corvids. Unfortunately, to our knowledge not enough relevant data on corvids are available for comparison.

### Sociality and other ecological conclusions

Our results strengthen the view that social groups are in fact family groups. Certain individuals were fed by others, and all the groups we caught were mixed-sex. It is interesting to note that the normal clutch size of one or two eggs plus two parents would produce the very commonly seen group sizes of three or four. One of our male Crows in captivity has continued to feed two of the others with which it was caught, and we have also observed another bird being

fed (but were unable to identify the individuals involved). This provides further evidence that families stay together in the wild. However, we have not yet performed any genetic analyses for relatedness, which should be conclusive.

We observed no physical aggression in the wild except for dominance interactions around food, despite often seeing several groups in the same area. However, when large numbers of Crows were together in close proximity they were often extremely noisy. On the basis of our observations, it therefore seems unlikely that the Crows defend any territorial boundaries with physical aggression, but that vocalizations may serve to enforce territories.

Although we know much of what makes up the Crows' diet, we have very little idea of the proportions of different components. It is noteworthy that carrion, which seems to be a major component of their diet, must be a recent addition, because the only large mammals on the island (pigs and deer) are introduced, and there are no large native mammals. The evolution of tool use in New Caledonian Crows could be related to this absence of native mammals: tool use allows the Crows to obtain protein-rich foods that are otherwise unavailable. Also absent from the native fauna are woodpeckers – whose wood-probing niche the Crows may partially occupy – although Horned Parakeets *Eunymphicus cornutus* might also compete in this niche (Orenstein 1972). We also speculate that the peculiar bill shape of the Crows may be related to their tool use. The straightness of the maxilla probably makes tool use easier, so a pre-existing straight bill may have promoted the emergence of tool use. Alternatively, the pre-existence of tool use may have been an evolutionary pressure on bill shape.

As this contribution testifies, virtually nothing is known about the ecology of the New Caledonian Crow and very little about its behaviour. Until now, in spite of the growing attention that this species has received because of its tool-oriented behaviour, even basic morphometric information was missing. We have summarized available information regarding their field biology, listed all the relevant literature and provided a set of basic measurements that we hope will serve as reference and orientation for further field studies.

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# APPENDIX 1

## Details of sexing by genetic analysis

The DNA was extracted using a chelex extraction technique (Walsh *et al.* 1991). Sex was determined by PCR amplification of the *CHD1-W* and *CHD1-Z* genes using P2 and P8 primers (Griffiths *et al.* 1998). Products were separated by electrophoresis through 4% polyacrylamide gels and visualized using silver staining (Bassam *et al.* 1991). Sex was determined by the presence/absence of the *CHD1-W* band: both sexes have the *CHD1-Z* band but only males have the *CHD1-W* band.

# APPENDIX 2

## Details of measurement methodology

See Table 2 for details of how most measurements were made. Wing profiles were obtained by holding the Crow against the side of a table, stretching one wing across a cardboard sheet on the table, spraying a mist of water on to the sheet and then sketching around the silhouette created (e.g. Shaffer *et al.* 2001). The profiles were scanned into a computer, and the wing length, root chord and area were measured using image analysis software (ImageJ 1.29x, by W. Rasband, National Institutes of Health, USA; http://rsb.info.nih.gov/ij). Total wing area ($S$) was calculated by doubling the single wing area, and adding the interwing area (estimated as the root chord $*$ body girth/$\pi$). Wing span ($b$) was calculated by doubling the wing length and adding the body girth/$\pi$. Aspect ratio ($A$) and wing loading ($W$) were then calculated ($A = b^2/S$, $W = N/S$, where $N$ is weight) (Pennycuick 1989).

All measurements were taken from the birds' right-hand sides. All measurements were taken by C.R., except weight, which was taken by B.K. C.R. and B.K. were blind to the sexes of birds at the time of measurement, except for two females that had been the subjects of previous behavioural experiments.