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Parallel tool industries in New Caledonian crows

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Individual specialization in the use of foraging tools occurs in hunter-gatherer societies but is absent in non-human primate tool use. 'Parallel tool industries' in hunter-gatherers are mainly based on strict sexual division of labour that is highly reliant on social conformity. Here, we show that 12 individuals in a population of New Caledonian crows on Maré Island had strong preferences for either stick tools or pandanus tools. Eight of the 12 crows had exclusive preferences. The individual specialization that we found is probably associated with different foraging niches. However, in spite of sexual size dimorphism there was no significant association between the sex of crows and their tool preferences. Our findings demonstrate that highly organized, strict sexual division of labour is not a necessary prerequisite for the evolution of parallel tool industries.

Keywords: *Corvus moneduloides*; New Caledonian crow; parallel tool industries; tool specialization; transmission mechanisms; vertical social learning

1. INTRODUCTION

Individual specialization in the use of foraging tools is associated with sophisticated material culture in highly organized hunter-gatherer societies (Bird 1999; Waguespack 2005). Such partitioning of foraging technology is only known to exist for certain from the Upper Paleolithic, where it creates 'parallel tool industries' (Waguespack 2005). These parallel tool industries are mainly a consequence of strict division of labour where females and males have different foraging niches (Bird 1999). For example, it is generally accepted that Clovis women specialized in collecting small game and plant material and Clovis men specialized in big-game hunting (Waguespack 2005). Non-human primate tool users like chimpanzees Pan troglodytes (McGrew 1992) and orangutans Pongo pygmaeus (Van Schaik & Knott 2001) lack consistent individual specialization in foraging tools.

An extraordinary feature of the behaviour of New Caledonian crows *Corvus moneduloides* (crow hereafter) is the manufacture of two very distinct types of foraging tool throughout their range: tools made from sticks and similar material (Hunt 1996; Hunt & Gray 2002), and those made from the barbed leaves of *Pandanus* species trees (Hunt 1996; Hunt & Gray 2003). In areas where both tool types are made on mainland Grande Terre, it is not uncommon to see an individual carrying a stick tool and another close by carrying a pandanus tool (G. R. Hunt 1993–1995, personal observation). The manufacture of both stick and pandanus tools in a crow population could occur if individuals simply foraged similarly across tree types using the nearest material for tools. That is, when a crow visited a *Pandanus* tree it used pandanus tools and when it foraged in other trees it used stick tools. The co-occurrence of stick and pandanus tools at sites could also be a consequence of specialization in foraging locations by adults. The different physical characteristics of stick and pandanus tools suggest that they may be used to capture a different subset of the available prey. In contrast to stick tools which are stiff and round, pandanus tools are flexible and flat (figure 1). Niche partitioning in birds is common where significant size dimorphism exists between males and females (Selander 1966). The different feeding niches are probably a consequence rather than a cause of sexual size dimorphism (Darwin 1871; Aulén & Lundberg 1991; Webster 1997). Niche partitioning associated with sexual size dimorphism may be related to morphological differences and/or competition for food (Noske 1986; Aulén & Lundberg 1991; Webster 1997; Pasinelli 2000; Radford & du Plessis 2003). Given that male crows are significantly larger than female crows (e.g. 10% difference in bill length and 24% difference in body weight) (Kenward et al. 2004), and breeding pairs stay together on home ranges year round (J. C. Holzhaider et al. unpublished data), niche partitioning within crow pairs is a distinct possibility. For example, the larger male bill may be more effective when foraging in non-Pandanus trees if this involves breaking up wood to extract prey as well as tool use.

To investigate if individual crows specialized in one type of tool, we documented the behaviour of freeliving mated crows extracting food at feeding tables on Maré Island, New Caledonia.

2. MATERIAL AND METHODS

At our study site on Maré Island from August 2003 to August 2006, we set up feeding tables in forest on which we placed dead logs drilled with vertical holes. The dimensions of the holes were consistently around 6-7 cm deep and 2.6 cm in diameter. We placed small pieces of meat in the holes and observed crows extracting it with tools (figure 1). Material for stick tools was readily available around tables, either lying on the ground or in trees. Pandanus trees are common at the site but patchily distributed. To ensure that crows at tables had ready access to both sticks and Pandanus leaves, we always stood a freshly cut whole Pandanus tree next to a table. When on a table, a crow could simply hop into the Pandanus tree tied to it to manufacture a tool. We documented crow behaviour at tables from nearby hides, either by direct observation or on video camera. Crows visited tables throughout the day, but most of the successful visits to tables were in the mornings.

Crows on Maré only manufacture non-hooked stick tools and wide pandanus tools, not the more complex hooked twig tools and stepped pandanus tools that birds produce on Grande Terre (Hunt 1996; Hunt & Gray 2002, 2003, 2004). We recorded stick-tool selection when a crow used a stick in a hole and obtained it away from the table or manufactured it. We recorded wide-pandanustool selection when a crow manufactured and then used one of these tools in a hole. This sampling regime therefore excluded cases where a crow used a tool that it found on the table. We recorded at most one stick and/or pandanus record per visit to a table by a crow. Of the 12 mated crows for which the sample size was sufficient for the analyses (greater than 9 records), only one was not individually colour-banded. However, we used data for the unbanded crow only when she visited tables with her banded partner and/or juvenile. 174 G. R. Hunt & R. D. Gray Parallel tool industries





Figure 1. A New Caledonian crow pair which exclusively selected either pandanus tools (female at left) or stick tools (male at right).

3. RESULTS AND DISCUSSION

All 12 crows had a significant preference for either stick (n=7) or pandanus (n=5) tools (figure 2); eight of the crows had an exclusive preference. In spite of the strong preferences, many of the 12 crows also sometimes used the non-preferred tool type when they found these tools on tables. The strong individual specialization that we found was unlikely to be related to factors like site or seasonal effects. This is because we collected data from individual crows at different feeding tables and in different months of the year, over a period of usually several years.

The individual specialization in the use of foraging tools by hunter-gatherers is associated with different foraging niches. We have insufficient direct observations to know if the 12 crows in this study specialized in feeding locations when foraging away from feeding tables. However, circumstantial evidence suggests, it is likely that the individuals which specialized in wide pandanus tools foraged more often in Pandanus trees than did the stick-tool specialists. At our study site, crows generally seem to use each tool type in different vegetation within the forest. Although we sometimes see crows using stick tools in Pandanus trees, they mainly use them in non-Pandanus trees. For example, we commonly find stick tools, and only very rarely wide pandanus tools (J. C. Holzhaider 2006, personal observation), at sites where crows have been extracting cerambycid larvae from dead wood. On the other hand, we frequently observe crows at our study site using wide pandanus tools in Pandanus trees to extract small invertebrates but not outside these trees. That we often find wide pandanus tools discarded in Pandanus trees suggests that crows rarely use them outside these trees.

In spite of sexual size dimorphism in crows and the circumstantial evidence that individual specialization was associated with different foraging niches, there was no significant relationship between the sex of crows and the type of tool that they preferred to use $(2 \times 2 \text{ contingency table with Fisher's exact probability test: 2-tailed <math>p=0.22$, n=12; figure 2). This shows that parallel tool industries in New Caledonian crows, and associated foraging niche partitioning, are not based on



Figure 2. The number of times that 12 mated crows obtained a stick tool (brown fill) or made a pandanus tool (green fill) to extract meat from holes at feeding tables. Labels on the *x*-axis indicate the sex and ID of crows (e.g. 'F1'=female 1). All but one of the 12 χ^2 -test *p*-values for tool-type preference were less than 0.0001; the *p*-value for crow M6 was less than 0.05. Paired crows were F1/M4, F2/M5, F3/M3 and F4/M1.

a rigid division of labour between the sexes. It is possible that sexual size dimorphism may have a weaker effect on the tool type that a crow prefers to use which is below the limit of our sample size to detect.

Humans have an evolved disposition for basic tool skills (Lockman 2000), but horizontal (peer-to-peer) social learning clearly plays a major role in determining which tool a hunter-gatherer uses. Social conformity is probably important in bringing about the strict sexual division of labour in subsistence seen in almost all hunter-gatherer societies (Bird 1999). In contrast, the parallel tool industries we have documented in crows could either be a consequence of genetic differences or different, vertically inherited (parent-to-offspring) social traditions. Kenward et al. (2006) have demonstrated that social learning can influence the development of stick-tool skills in young crows. An evolved disposition to develop basic stick tool use without social learning has also been demonstrated in juvenile crows, but there is little evidence that such a disposition exists for basic pandanus tool manufacture (Kenward et al. 2005; Hunt et al. in press). The social organization and development of crows is likely to promote vertical social learning and minimize opportunities for the horizontal transmission of tool manufacturing techniques. The crows at our study site on Maré spend most of their time in family units consisting of parents and dependent juveniles (J. C. Holzhaider et al. unpublished data). The juveniles develop tool skills during their first year in close association with parents. Early sensitive periods for acquisition of foraging skills have been documented in other birds (Tebbich et al. 2001) and would act to further minimize the possibility of horizontal transmission.

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