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### Enhanced social learning between siblings in common ravens, Corvus corax

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It has been suggested that social dynamics affect social learning but empirical support for this idea is scarce. Here we show that affiliate relationships among kin indeed enhance the performance of common ravens, *Corvus corax*, in a social learning task. Via daily behavioural protocols we first monitored social dynamics in our group of captive young ravens. Siblings spent significantly more time in close proximity to each other than did nonsiblings. We subsequently tested birds on a stimulus enhancement task in model—observer dyads composed of both siblings and nonsiblings. During demonstration the observer could watch the model manipulating one particular object (target object) in an adjacent room. After removing the model, the observer was confronted with five different objects including the former target object. Observers from sibling dyads handled the target object for significantly longer periods of time as compared with the other four available objects, whereas observers from nonsibling dyads did not show a preference for the target object. Also, siblings matched the model's decision to cache or not to cache objects significantly more often than did nonsiblings. Hence, siblings were likely to attend to both, the behaviour of the model (caching or noncaching) and object-specific details. Our results support the hypothesis that affiliate relations between individuals affect the transmission of information and may lead to directed social learning even when spatial proximity has been experimentally controlled for.

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Social learning, i.e. learning that is influenced by observation of, or interaction with, other individuals or their products (Galef 1988; Heyes 1994), has been found in a variety of animals including common ravens, *Corvus corax* (Fritz & Kotrschal 1999). Social dynamics, the distribution of social interactions within a group, could be critical for the pattern and type of social learning and for the spread of new behaviours in a group (Coussi-Korbel & Fragaszy 1995; Fritz & Kotrschal 2002).

Social dynamics may be characterized by social spacing and behavioural coordination in space and time (Coussi-Korbel & Fragaszy 1995). Social spacing has been defined as the 'differences in the frequency and degree of spatial

Correspondence and present address: C. Schwab, Konrad-Lorenz-Forschungsstelle für Ethologie, Fischerau 11, A-4645 Grünau, Austria (email: ch\_schwab@yahoo.com). T. Bugnyar is at the Department for Behaviour, Neurobiology and Cognition, Althanstr. 14, A-1090 Vienna, Austria. proximity sought and tolerated between individuals' (Coussi-Korbel & Fragaszy 1995, p. 1446) and behavioural coordination in space and time involves that 'an individual approaches the same site as another and engages in a similar activity simultaneously with the other at that site' (Coussi-Korbel & Fragaszy 1995, p. 1443). Therefore, the quality of social learning may vary between dyads depending on their social relations, whereby social dynamics may affect the salience of individuals for each other and the likelihood of preferential (Hatch & Lefebvre 1997) or directed social learning (Coussi-Korbel & Fragaszy 1995). For preferential or directed social learning to occur it is necessary that animals live in socially structured groups (e.g. kin and nonkin, familiar and unfamiliar) to provide individuals with opportunities to choose from alternative sources of information (Hatch & Lefebvre 1997). Furthermore, preferential or directed social learning indicates that particular models will be more influential for certain individuals than others (Coussi-Korbel & Fragaszy 1995; Laland 2004).

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In the present study we aimed to investigate preferential or directed social learning based on affiliate relations in juvenile common ravens. A number of variables have been shown to direct social learning, such as dominance (Nicol & Pope 1994, 1999), sex (Mason & Reidinger 1981; Benskin et al. 2002; Katz & Lachlan 2003), age (Galef & Whiskin 2004), kinship (Hatch & Lefebvre 1997), familiarity (Lachlan et al. 1998; Swaney et al. 2001; Benskin et al. 2002) and pair bonding (Wechsler 1988). Still, studies on the effects of affiliation (Russon & Galdikas 1995; Bonnie & de Waal 2006) on social learning are rare.

Ravens are well capable of learning socially from both, attached conspecifics (Fritz & Kotrschal 1999) and heterospecifics (M. Loretto, T. Bugnyar, K. Kotrschal, unpublished data). After becoming independent from their parents at about 100 days after hatching, they spend their first years in a nonbreeder-group until they form longterm monogamous pairs and establish territories at 3-4 years of age (Haffer & Bauer 1993). Such groups of juvenile nonbreeders provide the opportunity for developing diverse social relations with conspecifics. They are essentially fission-fusion societies with individuals assembling at overnight roosts and splitting into variable groups during daytime foraging (Heinrich et al. 1994; Ratcliffe 1997). Ravens of these groups recruit conspecifics via food calls to rich food sources (Heinrich 1988; Bugnyar et al. 2001), mainly to overcome defence by territorial pairs (Heinrich 1988; Marzluff & Heinrich 1991).

If those nonbreeder-groups would be just aggregations at carcasses or overnight roosts one could expect that the social relations are qualitatively similar between all individuals. But if the members of these groups would show some social ties (Heinrich 1988; Huber 1991; Parker et al. 1994) or even form socialized subgroups (Huber 1991) it could be expected that the social relations show different qualities between certain individuals. There would be the opportunity for individuals to develop different social relations. if they consistently interact with certain other individuals, and to use different sources of information provided by other individuals. Hence, the social ontogeny of ravens suggests that testing for preferential learning should be most promising during this nonbreeder period when individuals need to acquire information about the world.

Affiliate social relations can be characterized on a number of levels (Bonnie & de Waal 2006), such as high levels of sociopositive and low levels of agonistic behaviours. Thereby, sociopositive behaviours are measured as social support, food sharing or allopreening and agonistic behaviours as approach-retreat interactions or fights. Because of our short focal period (four months) in this study we concentrated on spatial proximity as an integrative measure (Bonnie & de Waal 2006) for determining social dynamics between individuals. Close social spacing and behavioural coordination in space and time do not only need social tolerance between individuals but also include actively seeking spatial proximity of others and can therefore, be regarded as basic measures of affiliation. We first examined the social dynamics within our group of hand-raised ravens via behavioural observations. We then experimentally tested for the influence of social

dynamics on social learning performance in a stimulus enhancement task. Following Zentall's (1996, p. 229) definition 'the term stimulus enhancement is used when the activity of the demonstrator draws the attention of the observer to a particular *object*' and it is considered to involve relatively low cognitive capacities (Galef 1988). Unlike previous experiments on ravens (Fritz & Kotrschal 1999) model-observer dyads were tested in physical separation to control for effects of spatial proximity on social learning. Following the ravens' life history in nonbreedergroups we expected that the social dynamics would not be randomly distributed in our group of juvenile handraised ravens. We predicted enhanced social learning performance when individuals in a model-observer dyad maintain affiliate relationships as compared with socially more distant dyads.

#### METHODS

#### Subjects and Keeping

Subjects were 12 juvenile common ravens, C. corax, that had been hand-raised in four sibling groups from 12 to 40 days after hatching to fledging at the Konrad-Lorenz-Research Station in Gruenau, Austria, in spring 2004. At the beginning of this study, birds were in their second month postfledging (fourth month of age). Seven birds (three males, four females) were zoo-bred (München, Wuppertal) and five birds (four males, one female) were taken out of wild nests with permission. At the time of the study birds were housed together in one social group in an aviary in the Cumberland game park in Gruenau, Austria, together with two adult male birds. They will remain in captivity until the end of their natural life span. The aviary consisted of three outdoor compartments (80, 80 and 35 m<sup>2</sup>, maximum height of 7 m) and of experimental compartments, consisting of a central room  $(16 \text{ m}^2)$ , two lateral chambers (left and right, each  $6 \text{ m}^2$ ) and two pathways (left and right, each  $4 \text{ m}^2$ ) which could all be divided by wire-mesh doors. Except of the experimental compartments the aviary was equipped with natural vegetation, wooden perches and rocks. In addition birds were provided with leafs, twigs and plastic toys for behavioural enrichment. Birds had ad libitum access to water and were fed three times a day with various kinds of meat, milk products, vegetables and fruits. They were marked with coloured rings for individual identification.

#### **Behavioural Observations**

We carried out behavioural observations twice a day, morning and afternoon, for 30 min. Observations consisted of 5-min focals and were counterbalanced for order of observations for each individual. We recorded all social interactions between the focal individual and any other conspecific. The observation period lasted from fledging of the birds, beginning of May 2004 to the end of the experimental trials, end of August 2004, resulting in an average number of focal observations of  $65.6 \pm 3.9$  (range: 58-71) and an average total observation time of Download English Version:

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