

Effects of Group Size on Approach to Novel Objects in Ravens (*Corvus corax*)

Mareike Stöwe*, Thomas Bugnyar*†, Bernd Heinrich† & Kurt Kotrschal*

* Konrad Lorenz Research Station, Grünau, Austria

† University of Vermont, Burlington, VT, USA

Correspondence

Mareike Stöwe, Konrad Lorenz Research Station, Grünau 11, A-4645 Austria.
E-mail: m_stoewe@hotmail.com

Received: March 19, 2006

Initial acceptance: April 21, 2006

Final acceptance: April 21, 2006 (M. Taborsky)

doi: 10.1111/j.1439-0310.2006.01273.x

Abstract

Neophobia may constrain explorative behaviour, learning and innovation, while social context may facilitate approach to novel objects and acceptance of novel food. We examined the effects of neophobia on the exploration of novel objects in relation to social context in ravens (*Corvus corax*). Ravens are suitable subjects for studying effects of social context, as they are highly neophobic scavengers that recruit conspecifics to food. We tested two groups of six and 11 hand-raised birds in three conditions: single-bird, in dyadic combinations and sibling subgroups of three to six birds. Contrary to expectation, individuals of both groups were quicker to approach novel objects when tested alone than when tested with conspecifics. However, they spent more time close to and manipulating the novel objects in the social conditions (dyadic and group) than when being alone. We discuss the possibility that the higher latencies of dyads and groups to approach novel objects may reflect a 'negotiation' process in a 'war of attrition' between the individuals over risk-taking.

Introduction

Barnett (1963) emphasized that a 'new object reaction' is temporary and elicited by a change in an otherwise familiar situation, while Greenberg & Mettke-Hoffmann (2001) considered similar behaviour as neophobia and defined it as 'the avoidance of an object or other aspect of the environment solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past'. Both definitions also include avoidance responses towards familiar objects at a different place. While neophobia may reduce exposure to danger, it can also limit explorative behaviour and constrain exploitation of novel food sources, learning and innovation (Seferta et al. 2001; Greenberg 2003; Reader & Laland 2003). Interspecific differences in neophobia depend on ecology and social organization (Fragaszy & Mason 1978; Greenberg

1983, 1990, 1992; Mettke-Hofmann et al. 2002; Day et al. 2003). On an individual level, the response to novel objects is also modulated by life-history stage (Heinrich 1995; Winkler & Leisler 1999) and social status (Katzir 1982, 1983; Stahl et al. 2001; Gómez-Laplaza 2002). In addition, individuals differ in suites of correlated behavioural and physiological parameters ('coping styles') leading to a cross-context consistency in how they deal with challenges (Koolhaas et al. 1999, review by Sih et al. 2004; Groothuis & Carere 2005).

One benefit of living in social groups is the potential advantage of learning when, how and what to feed (e.g. Galef & Giraldeau 2001), particularly when dealing with novel food (Galef 1993). The acceptance of novel food may be facilitated by observing conspecifics handling/eating it, as demonstrated in gerbils, *Meriones unguiculatus* (Forkman 1991), capuchin monkeys, *Cebus apella* (reviewed in Visalberghi &

Addressi 2003), red-winged blackbirds, *Agelaius phoeniceus* (Mason & Reidinger 1981), zebra finches, *Taeniopygia guttata* (Coleman & Mellgren 1994; Benskin et al. 2002, novel feeders), budgerigars, *Melopsittacus undulatus* (Soma & Hasegawa 2004) and Norway rats, *Rattus norvegicus* (Galef 1996). Social environment may also facilitate the approach to novel food/objects because individuals may be less stressed when tested in groups rather than when alone (Greenberg 1990; Marzluff & Heinrich 1991; Cadieu et al. 1995). Thus, proximally, social context may abbreviate approach latencies by lowering fear. On the ultimate level it may reduce risk by the dilution effect (Krause & Ruxton 2002). However, delay or even inhibition of approach/acceptance of novel food in a social context have also been observed (fish: Ryer & Olla 1991; Brown & Laland 2001, 2002, great tits: Oers van et al. 2005). Whether social environment speeds up or delays the use of novel food sources may depend on social dynamics (e.g. Chalmeau & Gallo 1993; Nicol & Pope 1994, 1999; Coussi-Korbell & Fragarzy 1995), age (e.g. Sasvári 1985) and on the profitability of scrounging (Barnard & Sibly 1981; Giraldeau & Lefebvre 1986, 1987; Fragarzy & Visalberghi 1989; Beauchamp & Kacelnik 1991; Fritz & Kotrschal 1999; Midford et al. 2000).

Ravens are scavengers that become highly neophobic when older than 1 mo post-fledging (Heinrich 1995; Heinrich et al. 1995; Kotrschal et al. 2001; Kijne & Kotrschal 2002). Their neophobia may have evolved in their coexistence with predators and potentially dangerous competitors such as wolves, *Canis lupus*, and in response to hundreds of years of human persecution. When independent from their parents, ravens assemble in non-breeder groups until pair formation at 3–4 yr of age (Glutz von Boltzheim & Bauer 1993; Ratcliffe 1997). Conspecifics, other birds and mammals (e.g. carrion crows, *Corvus corone*, wild boars, *Sus scrofa*, pers. obs., M.S.) and even potentially dangerous competitors (e.g. wolves, which potentially provide food for ravens, Promberger 1992; Bugnyar & Kotrschal 2001; Stahler et al. 2002) were observed to facilitate ravens' approaches to food sources. In addition, ravens recruit conspecifics at food bonanzas with a specific call (Heinrich 1988b, 1994; Heinrich & Marzluff 1995; Marzluff et al. 1996; Bugnyar et al. 2001), especially when predation risk is high (Bugnyar & Kotrschal 2001). Thus, it has been suggested that social foraging reduces neophobia in ravens (Marzluff & Heinrich 1991).

We tested the effects of group size on approach to and manipulation of novel objects in ravens. We

observed two groups of ravens in three conditions: single-bird, dyads and sibling sub-groups of 3–6 birds. As ravens actively recruit conspecifics and social context often facilitates approach to novel objects, we predicted ravens to be slowest in approach when alone and fastest when tested in groups. Because of effects of social facilitation, we also expected the birds to manipulate the novel objects longer in the group than in the single-bird and dyadic conditions.

Methods

Animals and Housing

In spring 2002, we hand-raised a group of six ravens (four males, two females) at the University of Vermont (UVM), Burlington, USA. The birds were taken from the wild (see Acknowledgements for permits) and were raised in a single nest. Once fledged, we kept them in a social group together with one adult male (4 yr of age) in order to contribute to appropriate socialization of the juveniles. Free-ranging juveniles join groups of non-breeders consisting of birds of various age classes, when independent from their parents. The aviary was situated in a wood close to Burlington. It was divided into three sections that were separated by wire mesh and doors (30, 100, 64 m², Bugnyar et al. 2004) and contained trees, branches, sticks, stones, a shallow pool for bathing, natural shadow, wooden breeding niches and had natural ground cover.

In spring 2004, we hand-raised another group of 13 ravens (seven males, six females) at the Konrad Lorenz Research Station (KLF), Upper Austria. These ravens were raised in four nests, positioned in a distance of approx 1 m from each other in an indoor aviary. The birds of two nests (containing four and three ravens) were zoo-bred, while the birds of the two other nests (containing three ravens each, one nest of three siblings, one nest with birds originating from three different nests) were taken from the wild (see Acknowledgements for permits). Just before fledging we transferred all the birds to one nest in an outdoor aviary at the Cumberland Game Park, Grünau, Upper Austria, where they remained thereafter. Once fledged, we kept them in one group with two adult males (9 and 4 yr of age). The aviary was divided into three sections separated by wire mesh (80, 35, 80 m²) and had experimental rooms, separated by wooden walls and opaque doors. The aviary was structured with trees, branches, stones, tree trunks and shallow pools for bathing. The floor had

natural grass ground cover and gravel cover in the experimental rooms.

Birds of both years were marked with coloured leg rings for individual identification. Except for the experiments, they had access to all compartments of the aviary. Birds were fully habituated to short separations from the group, which was a standard procedure in previous experiments. The ravens were fed twice per day (morning and afternoon after the experiments) with meat, milk products and kitchen scraps. Water was provided *ad libitum*. After this series of experiments birds remained in the aviaries for further studies.

Experimental Set-Up: UVM Ravens

Experiments were performed from September, when the young ravens were 6 mo old, to the end of November 2002. In total, we offered 126 different objects (bottles, boxes, bags, cans, candles, cups etc.) in a size range of 25–45 cm lengths. We tested all individuals with the same novel objects, but each object was presented only once per bird. In all tests, birds could watch the experimenter (M.S.) putting the objects in place. We tested the juveniles only.

We conducted novel object tests in three conditions: with a single bird, in dyads and in the entire group. The conditions of birds alone and dyadic combinations were also part of other studies (on individual differences in object exploration and on social learning/scrounging, respectively) and thus followed slightly different protocols (see below). Subjects were tested in the middle section (100 m²) of the aviary in physical, but not visual and acoustical isolation from the rest of the group. Tests were performed on a daily basis with the conditions being semi-randomised. Each bird took part in only one trial per day. Birds participated voluntarily. Each of the six birds was tested six times alone and in the entire group. We matched the number of novel objects with the number of birds in the test. In the group condition, objects were arranged in a line approx. 1 m apart in the middle of the test compartment. We did not distribute the novel objects all over the test compartment to give the birds the opportunity to keep a large initial distance to the novel objects. Previous experiments showed that birds easily become distressed if the opportunity to keep distance to novel objects is not provided.

In the dyadic condition, each bird was tested once with every other juvenile of the group ($n = 5$ different combinations per bird). Here, we presented two identical sets of novel objects in a distance of 12 m

to one another, with two different novel objects per set, spaced 1 m apart. We offered two sets to prevent the dominant individuals from monopolising the access to the novel objects for subordinates. For reasons not related to this experiment, we used two sets of objects per trial, with each set consisting of two different novel objects, instead of only two identical novel objects. In a pilot study we found that two objects per set instead of one had no significant effect on approach behaviour. For data collection and analysis each set of objects was treated as one. Tests with a single bird were terminated after 6 min, whereas tests in the group and in dyadic combinations lasted for 20 min. We accounted for this time difference by restricting the comparison between all three conditions to the first 6 min of the trials. When comparing the dyadic condition to the group condition we included the data of the entire 20 min. In all conditions recordings were done directly by the experimenter (M.S.), standing next to the aviary. In the group condition an additional observer (T.B.) who was equally familiar with the birds helped with data collection.

Experimental Set-Up: KLF Ravens

We replicated the novel object tests with the KLF ravens, from beginning of September to the beginning of November 2004. As with the Vermont ravens, our subjects were 6 mo of age when we started the experiments. In total, we offered 4 different objects in the single-bird condition, 15 in the dyadic condition, 4 in the sibling sub-group condition and 4 when testing the entire group with one novel object at a time. Tests were performed with some methodological differences compared to the tests conducted at UVM.

Subjects were tested in one of the large outdoor-sections (80 m²) in visual and physical but not acoustical isolation from conspecifics. We performed novel object tests in four different conditions: with a single bird, in dyads, in sibling sub-groups (two groups of three and one consisting of four siblings) and in the entire group. In all conditions trials lasted for 20 min. In the single-bird and group conditions we conducted four novel object tests each. In dyadic combinations we combined each bird with every other juvenile of the group resulting in 55 dyads (10 tests per bird).

We matched the number of novel objects to the number of birds in the test in order to minimize competition over access to novel objects. Thus we used two equal novel objects in the dyadic condition

and three or four in the sub-group condition (depending on sibling group size). One juvenile female was excluded from all experiments since she was ill during the nestling period and showed retarded development. She was kept together with a juvenile male of the same nest in a separate aviary. Hence, we performed the dyadic tests with 11 birds. 10 of these 11 ravens had siblings that were kept in the same aviary. Thus, we conducted the novel object tests in sibling sub-groups with 10 birds. When comparing between conditions, we excluded the data of the raven which was not tested in sibling sub-groups.

To test for effects of the number of novel objects presented, we additionally conducted four novel object tests with the entire group ($n = 11$ birds), offering only one novel object at a time. In this condition we only measured approach latencies of every individual. We compared the approach latencies to the novel objects between sibling sub-groups and the entire group. Birds approached the novel objects significantly faster in the sibling sub-groups with several equal novel objects offered than when tested in the entire group with one novel object only (Wilcoxon, $n = 10$, $z = -2.70$, $p = 0.007$).

Due to stones and tree trunks in the aviary, the central part of the compartment was not fully visible from outside the aviary. Hence, in all conditions data were taken by M.S. from one position inside the aviary. Birds were habituated to observers collecting data from this specific position.

Behavioural Recordings

For both groups of birds we recorded the following behaviours: (a) approach latency (in s, distance to the novel object < 1 m); (b) approach frequency; (c) time spent close (< 1 m) to the novel object (in s); (d) duration of novel object manipulation (=novel object exploration, in s); (e) number of 'jumping jacks' (sensu Heinrich 1988a), i.e. when an individual jumped back with a wing flap, while approaching a novel object; (f) number of threat-retreat interactions, which are agonistic interactions; (g) duration birds spent sitting close to each other (distance < 50 cm), which we took as an indicator for socio-positive relationships.

Analysis

We calculated means per individual over trials. In the UVM ravens, we used data of the first 6 min per trial, to match different observation times when

comparing between the single-bird condition and those with conspecifics (dyads, group). Since individuals did not always approach or manipulate the novel objects during the test period, we calculated latency-scores instead of using exact latency times. Thereby we avoided cutting the distribution of latency times at the upper end (by accepting 6 min: for data of UVM ravens, or 20 min: for data of KLF ravens, in case the individuals did not approach the novel objects). Scores were calculated by dividing the number of trials with approach by the sum of latencies of all trials [=sum of latency times when the birds approached plus 6 min (UVM ravens) or 20 min (KLF ravens) for each trial the birds did not approach, Theobald & Goupillot 1990].

Data were analysed using the software package SPSS 9.0.1 (SPSS 1999) and by hand according to Siegel & Castellan (1988, Friedman two-way analysis of variance by ranks, when with a posthoc test for multiple comparisons). All test results are two-tailed. Results are reported as trends if $0.05 < p < 0.1$. Ravens of the UVM group rarely manipulated the novel objects. Therefore we only present data of the time the birds spent close to the novel objects. In the KLF group time spent close to the novel objects correlated with duration of novel object manipulation in each condition (Spearman rank-order correlation: single-bird: $n = 11$, $r_s = 0.94$, $p < 0.001$, dyads: $n = 11$, $r_s = 0.82$, $p = 0.002$, group: $n = 10$, $r_s = 0.99$, $p < 0.001$). We present data of time spent close to novel objects to allow comparisons between UVM and KLF data sets.

Results

Ravens of both groups showed similar patterns in approach and exploratory behaviour in the three conditions: single-bird, dyads and group. Birds approached the novel objects faster when alone than when with conspecifics (Fig. 1a), but spent less time close to the novel objects when alone (Fig. 1b). We summarize the results of between condition comparisons for each group (UVM and KLF ravens) in Table 1.

In both groups individual variation in response to the novel objects was high within conditions. We present results of Friedman two-way analysis of variance by ranks of between individual differences in each group in Table 2. However, individuals of both groups tended to show some consistency over the different test conditions in their approach behaviour to novel objects. Results of Spearman rank-order correlations are presented in Table 3.

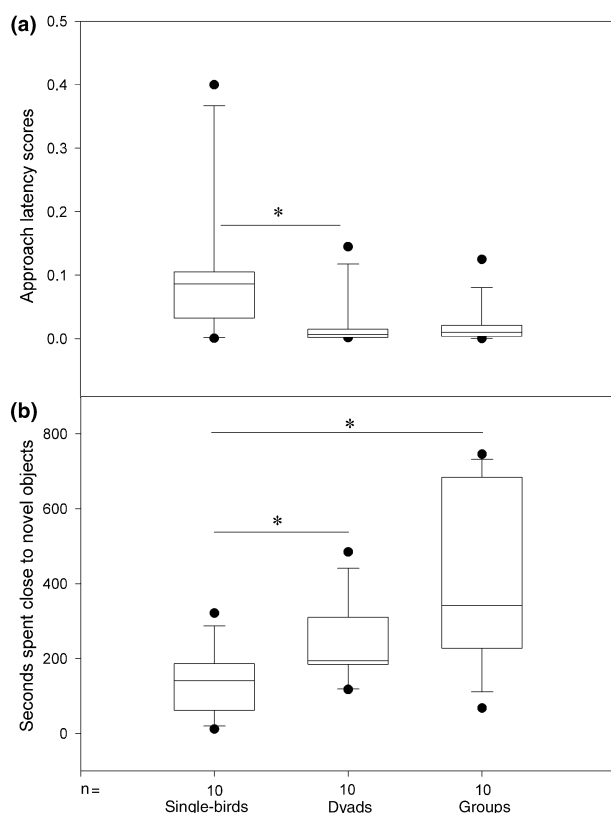


Fig. 1: Raven group at the Konrad Lorenz Research Station: comparison between social conditions: (a) approach latency score (Theobald & Goupillot 1990): the higher the score, the faster individuals approached the novel objects; (b) time spent close to novel objects in seconds, N = number of birds tested, box plots show the median and the interquartile range from the 25th to the 75th percentile. Whiskers above and below the box indicate the 10th and the 90th percentiles. Circles visualize outliers. Asterisks indicate significant between-condition differences as determined by Posthoc tests for multiple comparisons for Friedman two-way analyses of variance by ranks (* $p < 0.05$)

Agonistic interactions were rare in both groups (number of threats, UVM ravens in dyads: $\bar{X} = 1.47 \pm 1.96$, all after the first 3 min; in groups: $\bar{X} = 0.33 \pm 0.52$ occurring after the first 6 min; KLF ravens in dyads: $\bar{X} = 1 \pm 1.5$, all after the first 3 min; in groups: $\bar{X} = 1 \pm 1.4$, all after the first 3 min). Birds showed socio-positive behaviours mainly after approaching the novel objects. In the UVM ravens the approach frequency peaked in min 2, whereas the duration of sitting close to each other peaked in min 6 and remained higher thereafter than during the first 5 min of the trials (Fig. 2a). The KLF ravens approached the novel objects most often during the first minute of the trials, whereas the duration of sitting close to each other peaked in min 19 (Fig. 2b). In the second half of the 20-min

trials, KLF ravens (Wilcoxon test: $n = 11$, $z = -2.40$, $p = 0.016$) spent significantly more time sitting close to each other than in the first half, while this was not the case in UVM ravens (Wilcoxon test: $n = 6$, $z = -0.94$, $p = 0.34$).

Discussion

Ravens actively recruit conspecifics at ephemeral food sources (Heinrich 1988b, 1994; Heinrich & Marzluff 1991) and are attracted to feeding sites by the presence of conspecifics (Heinrich et al. 1993) and heterospecifics (Stahler et al. 2002). Therefore, we expected the birds to explore novel objects more readily when in dyads or in groups than when being alone. However, ravens of the KLF group approached the novel objects faster in the single-bird condition than when tested with conspecifics. The differences between conditions did not reach significance level in the UVM group. Test trials of the UVM ravens lasted for only 6 min in the single-bird condition and individuals did not always approach, which might account for less pronounced differences between conditions. Whenever UVM ravens did approach novel objects, they did so faster when tested alone.

A delayed approach when with conspecifics would have been expected, if in a social context the ravens interacted with each other and were thereby distracted from exploring the novel objects. However, both socio-positive and agonistic interactions started only after the peak in approach frequency, which renders this explanation unlikely.

We suggest instead that the delayed approach to the novel objects could be due to a 'negotiation process' over risk taking with one bird waiting for the other to take the lead. Upon introduction of the novel objects, the birds interrupted all normal activities such as handling familiar objects and social interactions until one bird initiated approaching the novel objects. This might to some extent be a 'war of attrition' (e.g. Maynard Smith 1974; Hammerstein & Parker 1982), with the individual that waits longer having the advantage to avoid potential risk, while the one approaching the novel objects first may take advantage of prime access to a potential resource. One of us (B. H.) observed in adult free-ranging ravens in Maine (USA) that dominants allowed the subordinates to approach a new pile of meat first, although they went first if there was only a small amount of meat available that one raven could carry away. This indicates that the balance between risk and benefit may affect who approaches first. Green-

Table 1: Comparison of behaviours between the three test conditions: single-bird (s.b.), dyadic and group (in both, UVM and KLF ravens)

Raven group	Test duration (min)	Behaviour	Single-bird–dyad–group	Single-bird–dyad	Single-bird–group	Dyad–group
			Friedman test	Posthoc test for multiple comparisons		
UVM	6	Approach latency (scores)	$n = 6, \chi^2_2 = 2.52, p > 0.05$	–	–	–
KLF	20	Approach latency (scores)	$n = 10, \chi^2_2 = 10.40, p < 0.01$	$p < 0.05$, s. b. < dyads	$p < 0.1$, s. b. < group	$p > 0.1$
UVM	6	Approach frequency	$n = 6, \chi^2_2 = -2.84, p > 0.05$	–	–	–
KLF	20	Approach frequency	$n = 10, \chi^2_2 = 10.55, p < 0.01$	$p > 0.1$	$p > 0.1$	$p < 0.05$ dyads > group
UVM	6	Time spent close (s)	$n = 6, \chi^2_2 = 2.92, p > 0.05$	–	–	–
KLF	20	Time spent close (s)	$n = 10, \chi^2_2 = 9.8, p < 0.02$	$p < 0.05$ s. b. < dyads	$p < 0.05$ s. b. < group	$p > 0.1$
UVM	6	Number of jumping jacks	$n = 6, \chi^2_2 = 5.19, p < 0.1$	$p < 0.05$ s. b. > dyads	$p > 0.1$	$p > 0.1$
KLF	20	Number of jumping jacks	$n = 10, \chi^2_2 = 9.80, p = 0.01$	$p < 0.05$ s. b. > dyads	$p < 0.05$ s. b. > group	$p > 0.1$
UVM	20	Approach frequency		Wilcoxon test: dyadic group condition		
UVM	20	Time spent close (s)		$n = 6, z = -1.99, p = 0.046$, dyad < group		
UVM	20	Number of jumping jacks		$n = 6, z = -1.78, p = 0.078$, dyad < group		
				$n = 6, z = -1.21, p = 0.22$		

We used Friedman two-way analysis of variance by ranks and posthoc test for multiple comparisons to test for between condition differences. Wilcoxon matched-pairs signed-ranks tests were used for comparison between dyadic and group condition in the UVM ravens. N = number of birds tested, $df = 2$ in all Friedman tests.

Table 2: Between individual differences in the three conditions, single-bird, dyadic and group.

Raven group	Behaviour	Single-bird	Dyad	Group
UVM	Approach latency (s)	$df = 5, \chi^2_6 = 18.12, p = 0.003$	$df = 5, \chi^2_5 = 4.22, p = 0.52$	$df = 5, \chi^2_6 = 6.09, p = 0.30$
KLF	Approach latency (s)	$df = 10, \chi^2_4 = 19.06, p = 0.039$	$df = 10, \chi^2_{10} = 33.36, p < 0.001$	$df = 9, \chi^2_4 = 28.17, p = 0.001$
UVM	Approach frequency	$df = 5, \chi^2_6 = 13.03, p = 0.023$	$df = 5, \chi^2_5 = 5.08, p = 0.41$	$df = 5, \chi^2_6 = 14.72, p = 0.012$
KLF	Approach frequency	$df = 10, \chi^2_4 = 23.55, p = 0.015$	$df = 10, \chi^2_{10} = 15.79, p = 0.11$	$df = 9, \chi^2_4 = 9.98, p = 0.36$
UVM	Time spent close (s)	$df = 5, \chi^2_6 = 19.63, p = 0.001$	$df = 5, \chi^2_5 = 4.14, p = 0.53$	$df = 5, \chi^2_6 = 20.41, p = 0.001$
KLF	Time spent close (s)	$df = 10, \chi^2_4 = 30.61, p = 0.001$	$df = 10, \chi^2_{10} = 23.25, p = 0.010$	$df = 9, \chi^2_4 = 27.63, p = 0.001$

We used Friedman two-way analysis of variance by ranks for comparison between the individuals. Test duration was 20 min in all conditions except for the UVM ravens in the single-bird condition, there tests lasted for 6 min. Chi-squared test subscripts indicate the number of test trials per bird.

Table 3: Consistency in individuals' approach behaviour to novel objects over the three test conditions, single-bird, dyadic and group

Raven group	Behaviour	Single-bird–dyad	Single-bird–group	Dyad–group
UVM	Approach latency (score)	$n = 6, r_s = 0.79, p = 0.062$	$n = 6, r_s = 0.13, p = 0.80$	$n = 6, r_s = 0.43, p = 0.40$
KLF	Approach latency (score)	$n = 11, r_s = 0.54, p = 0.087$	$n = 10, r_s = -0.57, p = 0.089$	$n = 10, r_s = -0.62, p = 0.054$
UVM	Approach frequency	$n = 6, r_s = 0.52, p = 0.28$	$n = 6, r_s = 0.82, p = 0.045$	$n = 6, r_s = 0.87, p = 0.025$
KLF	Approach frequency	$n = 11, r_s = -0.10, p = 0.77$	$n = 10, r_s = -0.30, p = 0.40$	$n = 10, r_s = 0.20, p = 0.58$
UVM	Time spent close (s)	$n = 6, r_s = 0.79, p = 0.062$	$n = 6, r_s = -0.81, p = 0.051$	$n = 6, r_s = -0.65, p = 0.26$
KLF	Time spent close (s)	$n = 11, r_s = 0.57, p = 0.066$	$n = 10, r_s = 0.48, p = 0.16$	$n = 10, r_s = 0.37, p = 0.29$

We compared individual responses between conditions using Spearman rank-order correlations. For correlations with behaviour in the single-bird condition in the UVM ravens we used only data of the first 6 min of the test trials in the dyadic and group condition.

berg & Mettke-Hoffmann (2001) hypothesised that if pay-offs are asymmetrical and the rank hierarchy is linear, subordinates should take the risk to approach first. This has been observed in several studies (e.g. response to novel space in jackdaws, *Corvus monedula*, Katzir 1982, predator inspection in angelfish, *Pterophyllum scalare*, Gómez-Laplaza 2002). With one

exception, dominant ravens of our tests did not approach first when being in groups.

The delayed approach to novel objects when together with conspecifics could be due to an increase in neophobia and thus social inhibition, as it was found in fish such as chum salmon, *Oncorhynchus keta*, and the atlantic salmon, *Salmo salar*, in

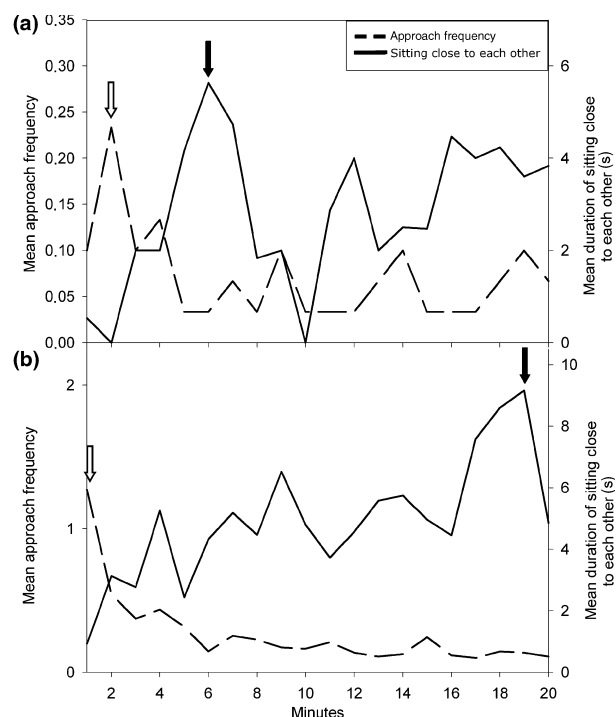


Fig. 2: Approach frequency and time spent close to each other in the dyadic condition for. (a) UVM ravens and, (b) KLF ravens. x-axis: minutes during the test trials. Hatched lines show mean number of approaches of all individuals taken together (y-axes left), solid lines visualize mean duration birds spent sitting close to each other (<50 cm) in seconds (y-axes right). White arrows indicate peak in approach frequency, black arrows point at peak in duration of sitting close to each other

which social context delayed or even inhibited approach to, and intake of, novel food (Ryer & Olla 1991; Brown & Laland 2001, 2002). When approaching a novel object ravens do jumping-jacks and thereby test, whether the object is potentially dangerous (Heinrich 1988a). In our study, the ravens conducted significantly more jumping-jacks when approaching the novel object alone than when being with conspecifics. This indicates that they approached more cautiously when being alone and supports our 'negotiation hypothesis', where one raven waits for the other to be the first and take the risk. If the delayed approach when tested with conspecifics would be due to a contagion of fear, we would expect to observe more jumping-jacks in the social conditions as compared to the single-bird condition. This was not the case.

We matched the number of novel objects with the number of birds in each test, to minimize potential effects of competition over novel objects. It is possible that a larger number of novel objects may

increase neophobia, which would mean that our results of approach latency may be an artefact. However, we argue that this explanation is unlikely. When we tested the entire KLF group with only one novel object, the birds approached the novel object significantly later than when tested in sibling sub-groups with the number of objects being equal to the number of birds. The appropriate control would have been testing the sibling sub-groups with one novel object only and not the entire group to keep group composition constant. Still, if the number of objects would determine approach latency, ravens should have been faster when tested in the entire group with one novel object than when being in sibling sub-groups with several novel objects, which was not the case.

In contrast to our results, Marzluff & Heinrich (1991) found that ravens approached new piles of meat quicker when in the group than alone. This was interpreted as a decrease of neophobia due to the presence of conspecifics. They worked with wild ravens which were trapped and habituated to the aviary before the onset of the experiments. Despite habituation to living in the aviary, the birds might have still been stressed by the isolation from the other birds and may therefore have been slower when approaching the new food piles alone compared to when being with conspecifics. In fact, the formerly free-ranging ravens flushed away from the food more often when being alone than when being with conspecifics. Our ravens were habituated to being in an aviary and to being temporarily separated from conspecifics.

The behavioural phenotype of individuals (Koolhaas et al. 1999) may be an important component determining exploratory behaviour in ravens. Indeed, individuals of both groups differed significantly in their response to novel objects. Within individuals we observed some consistency: birds readily approaching and staying close to novel objects in the single-bird condition tended to do so in the dyadic condition. However, when tested in groups individuals partly differed in their approach patterns compared to when tested alone or in dyads. These within-individual variance might be due to effects of social status and the sex of the birds they were combined with (Stöwe *et al.* 2006). This influence of social context might increase with group size. In addition, individuals also vary in their response to a social setting depending on their coping style (Oers van et al. 2005). These factors might account for the observed inconsistencies in approach behaviour of the birds when tested with conspecifics.

Although the presence of conspecifics (in dyads and groups) delayed the initial approach to novel objects, once a raven approached, it facilitated exploration (ravens spent more time close to and manipulating novel objects in the presence of conspecifics). Facilitating effects were more pronounced in group sizes >2. Since non-breeding ravens regularly forage in groups and actively recruit conspecifics at food sources, the potential benefits of feeding in a group (Heinrich & Marzluff 1995) seem to outweigh the disadvantage of a delayed initial approach.

In conclusion, when there are individuals in the group which approach novel objects quickly (due to their coping style, their experience or other factors), their presence may increase the motivation of others to approach as well. On the functional level, social context may dilute risk. However, the presence of some more nervous conspecifics may also lead to an increase in neophobia and inhibit or delay the approach. Alternatively, our results may reflect a strategic decision of the birds instead of a proximate constraint. An individual being tested alone must take the risk if interested in using a resource, while when others are present, it might wait until one of them takes the risk of prime exploration (war of attrition).

Apparently, there is no simple answer to the question of whether social context facilitates or inhibits the approach and exploration of novel objects, because it will depend on the species, group composition, individual dispositions and on individual decisions.

Acknowledgements

We acknowledge support by the University of Vienna, research grant for M. Stöwe, and by the FWF (P16939 B03) and the research grant for T. Bugnyar (E. Schrödinger J2064, 2225). We thank W. Forstmeier and G. Gaydon for comments and special thanks (by M.S.) to both families Bugnyar and Heinrich for their warmth and hospitality. Permanent support was provided by the Verein der Förderer der Konrad Lorenz Forschungsstelle and the Herzog von Cumberland Stiftung. We thank the zoos of Munich and Wuppertal, Germany, and P. Sömmmer for the supply with raven nestlings. Collecting and study permits for ravens include US Federal Fish and Wildlife Permit MB689376-0, State of Maine Department of Inland Fisheries and Wildlife Permit 22077, the Vermont Fish and Wildlife Department Scientific Collecting Permit to B.H. and the permit by the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg of

February the 25th, 2004. We thank Michael and Barbara Taborsky and two anonymous referees for constructive comments on earlier drafts of the manuscript.

Literature Cited

- Barnard, C. J. & Sibly, R. M. 1981: Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Anim. Behav.* **29**, 543–550.
- Barnett, S. A. 1963: *A Study in Behaviour*. The Camelot Press Ltd., London, pp. 28–33.
- Beauchamp, G. & Kacelnik, A. 1991: Effects of knowledge of partners on learning rates in zebra finches, *Taeniopygia guttata*. *Anim. Behav.* **41**, 247–253.
- Benskin, C. McW. H., Mann, N. I., Lachlan, R. F. & Slater, P. J. B. 2002: Social learning directs feeding preferences in the zebra finch, *Taeniopygia guttata*. *Anim. Behav.* **64**, 823–828.
- Brown, C. & Laland, K. 2001: Social learning and life skills training for hatchery reared fish. *J. Fish Biol.* **59**, 471–493.
- Brown, C. & Laland, K. 2002: Social enhancement and social inhibition of foraging behaviour in hatchery reared Atlantic salmon. *J. Fish Biol.* **61**, 987–998.
- Bugnyar, T. & Kotrschal, K. 2001: Movement coordination and signalling in ravens (*Corvus corax*): an experimental field study. *Acta Ethol.* **3**, 101–109.
- Bugnyar, T., Kijne, M. & Kotrschal, K. 2001: Food calling in ravens: are yells referential signals? *Anim. Behav.* **61**, 949–958.
- Bugnyar, T., Stöwe, M. & Heinrich, B. 2004: Ravens, *Corvus corax*, follow gaze direction of humans around obstacles. *Proc. R. Soc. Lond. B* **271**, 1331–1336.
- Cadieu, J. C., Cadieu, N. & Lauga, J. 1995: Local enhancement and seed choice in the juvenile canary, *Serinus canarius*. *Anim. Behav.* **50**, 793–800.
- Chalmeau, R. & Gallo, A. 1993: Social constraints determine what is learned in the chimpanzee. *Behav. Proc.* **28**, 173–188.
- Coleman, S. L. & Mellgren, R. L. 1994: Neophobia when feeding alone or in flock in zebra finches, *Taeniopygia guttata*. *Anim. Behav.* **48**, 903–907.
- Coussi-Korbell, S. & Frigaszy, D. M. 1995: On the relationship between social dynamics and social learning. *Anim. Behav.* **50**, 1441–1453.
- Day, R. L., Coe, R. L., Kendal, J. R. & Laland, K. N. 2003: Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Anim. Behav.* **65**, 559–571.
- Fragaszy, D. M. & Mason, W. A. 1978: Responses to novelty in *Saimiri* and *Callicebus*: Influence of social context. *Primates* **19**, 311–331.

- Fragaszy, D. M. & Visalberghi, E. 1989: Social influences on the acquisition of tool-using behaviour in tufted capuchin monkeys (*Cebus apella*). *J. Comp. Psychol.* **103**, 159–170.
- Fritz, J. & Kotrschal, K. 1999: Social constraints and profitability of scrounging affect social learning. In: Proceedings of the AISB'99 Symposium on Imitation in Animals and Artefacts, 6th–9th April (Dautenhahn, K. & Nehaniv, C., eds). The Society for the Study of Artificial Intelligence and Simulation of Behaviour, Edinburgh, pp. 20–26.
- Forkman, B. 1991: Social facilitation is shown by gerbils when presented with novel but not with familiar food. *Anim. Behav.* **42**, 860–861.
- Galef, B. G. Jr 1993: Function of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Anim. Behav.* **46**, 257–265.
- Galef, B. G. Jr 1996: Social enhancement of food preferences in Norway rats: a brief review. In: Social Learning in Animals, the Roots of Culture (Heyes, C. M. & Galef, B. G. Jr, eds). Academic Press, San Diego, pp. 49–64.
- Galef, B. G. Jr & Giraldeau, L. A. 2001: Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* **61**, 3–15.
- Giraldeau, L. A. & Lefebvre, L. 1986: Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Anim. Behav.* **34**, 797–803.
- Giraldeau, L. A. & Lefebvre, L. 1987: Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Anim. Behav.* **35**, 387–394.
- Glutz von Boltzheim, U. N. & Bauer, K. M. 1993: Handbuch der Vögel Mitteleuropas. Band 13/III, Passeriformes (4.Teil). Aula Verlag, Wiesbaden, pp. 2018.
- Gómez-Laplaza, L. M. 2002: Social status and investigatory behaviour in the angelfish (*Pterophyllum scalare*). *Behaviour* **139**, 1469–1490.
- Greenberg, R. 1983: The role of neophobia in foraging specialisation of some migrant Warblers. *Am. Nat.* **122**, 444–453.
- Greenberg, R. 1990: Ecological plasticity, neophobia and resource use in birds. *Stud. Avian Biol.* **13**, 431–437.
- Greenberg, R. 1992: Differences in neophobia between naive song and swamp sparrows. *Ethology* **91**, 17–24.
- Greenberg, R. 2003: The role of neophobia and neophilia in the development of innovative behaviour of birds. In: Animal Innovation (Reader, S. M. & Laland, K. N., eds). Oxford University Press, Oxford, pp. 175–197.
- Greenberg, R. & Mettke-Hoffmann, C. 2001: Ecological aspects of neophobia and neophilia in birds. *Curr. Ornithol.* **16**, 119–169.
- Groothuis, T. G. G. & Carere, C. 2005: Avian personalities: characterization and epigenesis. *Neurosci. Biobehav. Rev.* **29**, 137–150.
- Hammerstein, P. & Parker, G. A. 1982: The asymmetric war of attrition. *J. Theor. Biol.* **96**, 647–682.
- Heinrich, B. 1988a: Why do ravens fear their food? *Condor* **90**, 950–952.
- Heinrich, B. 1988b: Winter foraging at carcasses by three sympatric corvids, with emphasis on recruitment by the raven (*Corvus corax*). *Behav. Ecol. Sociobiol.* **23**, 141–156.
- Heinrich, B. 1994: Does the early raven get (and show) the meat? *Auk* **111**, 764–769.
- Heinrich, B. 1995: Neophilia and exploration in juvenile Common Ravens, *Corvus corax*. *Anim. Behav.* **50**, 695–704.
- Heinrich, B. & Marzluff, J. M. 1991: Do common ravens yell because they want to attract others? *Behav. Ecol. Sociobiol.* **28**, 13–22.
- Heinrich, B. & Marzluff, J. M. 1995: Why ravens share? *Am. Sci.* **83**, 342–350.
- Heinrich, B., Marzluff, J. M. & Marzluff, C. S. 1993: Common ravens are attracted by appeasement calls of food discoverers when attacked. *Auk* **110**, 247–254.
- Heinrich, B., Marzluff, J. M. & Adams, W. 1995: Fear and food recognition in naive common ravens. *Auk* **112**, 499–503.
- Katzir, G. 1982: Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L., I. Response to novel space? *Behaviour* **82**, 231–263.
- Katzir, G. 1983: Relationships between social structure and response to novelty in captive jackdaws, *Corvus monedula* L., II. Response to novel palatable food? *Behaviour* **86**, 183–208.
- Kijne, M. & Kotrschal, K. 2002: Neophobia affects choice of food item size in group-foraging common ravens (*Corvus corax*). *Acta Ethol.* **5**, 13–18.
- Koolhaas, J. M., Korte, S. M., de Boer, S. F., van der Vegt, B. J., van Reenen, C. G., Hopster, H., de Jong, I. C., Ruis, M. A. W. & Blokhuis, J. H. 1999: Coping styles in animals: current status in behaviour and stress-physiology. *Neurosci. Biobehav. Rev.* **23**, 925–935.
- Kotrschal, K., Bugnyar, T. & Stöwe, M. 2001: Kognition und Neophobie bei Raben. *Charandrius* **3**, 127–135.
- Krause, J. & Ruxton, G. D. 2002: Living in Groups. Oxford Univ. Press, Oxford.
- Marzluff, J. M. & Heinrich, B. 1991: Foraging by common ravens in the presence and absence of territory holders: an experimental analysis of social foraging. *Anim. Behav.* **42**, 755–770.
- Marzluff, J. M., Heinrich, B. & Marzluff, C. S. 1996: Raven roosts as mobile information centers. *Anim. Behav.* **51**, 83–103.
- Mason, J. R. & Reidinger, R. F. Jr 1981: Effects of social facilitation and observational learning on feeding beha-

- viour of the red-winged blackbird (*Angelaius phoeniceus*). *Auk* **98**, 778–784.
- Maynard Smith, J. 1974: The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209–221.
- Mettke-Hofmann, C., Winkler, H. & Leisler, B. 2002: The significance of ecological factors for exploration and neophobia in parrots. *Ethology* **108**, 249–272.
- Midford, P. E., Hailman, J. P. & Woolfenden, G. E. 2000: Social learning of a novel foraging patch in families of free-living Florida scrub-jays. *Anim. Behav.* **59**, 1199–1207.
- Nicol, C. J. & Pope, S. J. 1994: Social learning in small flocks of laying hens. *Anim. Behav.* **47**, 1289–1296.
- Nicol, C. J. & Pope, S. J. 1999: The effects of demonstrator social status and prior foraging success on social learning in laying hens. *Anim. Behav.* **57**, 163–171.
- Oers van, K., Klunder, M. & Drent, P. J. 2005: Context dependence of avian personalities: risk-taking behaviour in a social and non-social situation. *Behav. Ecol.* **16**, 716–723.
- Promberger, C. 1992: Mitteilungen aus der Wildforschung: Wölfe und Raben im Yukon. *Der Oberösterreichische Jäger* **56**, 34–35.
- Ratcliffe, D. 1997: *The Raven*. Academic Press Inc., San Diego.
- Reader, S. M. & Laland, K. N. (eds.) 2003: *Animal Innovation*. Oxford Univ. Press, Oxford, pp. 3–39.
- Ryer, C. H. & Olla, B. L. 1991: Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Environ. Biol. Fishes* **30**, 317–323.
- Sasvári, L. 1985: Different observational learning capacity in juvenile and adult individuals of congeneric bird species. *Z. Tierpsychol.* **69**, 293–304.
- Seferta, A., Guay, P.-J., Marzinotto, E. & Lefebvre, L. 2001: Learning differences between Feral Pigeons and Zenaida Doves: the role of neophobia and human proximity. *Ethology* **107**, 281–293.
- Siegel, S. & Castellan, N. J. Jr 1988: *Nonparametric Statistics for the Behavioural Sciences*, 2nd edn. McGraw-Hill, Singapore.
- Sih, A., Bell, A. & Johnson, C. 2004: Behavioural syndromes: an ecological and evolutionary overview. *TREE* **19**, 372–378.
- Soma, M. & Hasegawa, T. 2004: The effects of social facilitation and dominance on foraging success of buderigars in an unfamiliar environment. *Behaviour* **141**, 1121–1134.
- SPSS 1999: *SPSS for Windows*, Version 9.0.1. SPSS, Inc, Chicago.
- Stahl, J., Tolsma, P. H., Loonen, M. J. J. E. & Drent, R. H. 2001: Subordinates explore but dominants profit: resource competition in high arctic barnacle goose flocks. *Anim. Behav.* **61**, 257–264.
- Stahler, D., Heinrich, B. & Smith, D. 2002: Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. *Anim. Behav.* **64**, 283–290.
- Stöwe, M., Bugnyar, T., Loretto, M.-C., Schloegl, C., Range, F. & Kotrschal, K. (2006): Novel object exploration in ravens (*Corvus corax*): effects of social relationships. *Behav. Proc.* **73**, 68–75.
- Theobald, C. M. & Goupillot, R. P. 1990: The analysis of repeated latency measures in behavioural studies. *Anim. Behav.* **40**, 484–490.
- Visalberghi, E. & Addessi, E. 2003: Social learning about food in capuchin monkeys. In: *The Biology of Traditions, Models and Evidence* (Fragaszy, D. M. & Perry, S., eds). Cambridge Univ. Press, Cambridge, pp. 187–212.
- Winkler, H. & Leisler, B. 1999: Exploration and curiosity in birds: functions and mechanisms. In: *Proceedings of the 22nd International Ornithology Congress* (Adams, N. J. & Slotow, R. H., eds). Birdlife South Africa, Durban, Johannesburg, pp. 915–932.