

# Behavioural phenotypes may determine whether social context facilitates or delays novel object exploration in ravens (*Corvus corax*)

Mareike Stöwe · Kurt Kotrschal

Received: 3 November 2006 / Accepted: 30 April 2007 / Published online: 20 July 2007  
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**Abstract** Individuals consistently differ in behavioural phenotypes. Here we examine the interaction between behavioural phenotype and response to social context during novel object exploration in a neophobic corvid species, the raven (*Corvus corax*). The presence of conspecifics tends to encourage object exploration and learning but may also delay or even inhibit exploratory behaviour. Factors such as individual differences in response to social context may determine whether the presence of a conspecific facilitates or inhibits approach to novel objects. We confronted eleven six-month-old hand-raised ravens with novel objects, both individually and in dyadic combinations. We defined individuals as “fast” and “slow” explorers on the basis of their approach latency to novel objects when tested individually. The presence of a conspecific delayed the approach of fast birds to novel objects. Slow birds, in contrast, approached the novel objects with lower latencies and spent more time close to them when in dyads with fast siblings than when alone. The individuals’ approach behaviour seemed to determine whether social context facilitated or delayed exploratory behaviour. This may contribute to explaining ambiguous results concerning the effects of social context in previous studies.

**Keywords** *Corvus corax* · Novel object exploration · Personality · Social facilitation

## Introduction

Individuals differ in suites of correlated behavioural and physiological characteristics (“behavioural syndromes”, “coping styles”) leading to a cross-context consistency in how they deal with challenges (Gosling and John 1999; Koolhaas et al. 1999; Sih et al. 2004; Groothuis and Carere 2005; Kralj-Fišer et al. 2006). These differences between behavioural phenotypes are genetically and epigenetically heritable (Dingemanse et al. 2002; Drent et al. 2003; Daisley et al. 2004; van Oers et al. 2004) and may affect dispersal (Armitage 1986; Dingemanse et al. 2003), dominance (Gómez-Laplaza 2002; Dingemanse and de Goede 2004), mate choice, reproductive success (Dingemanse et al. 2004, Both et al. 2005; van Oers et al. 2006), and survival (Cavigelli and McClintock 2003). Many studies on behavioural phenotypes in the social domain have focussed on aggressive behaviour (Benus et al. 1990; Verbeek et al. 1996; Benus 2001; D’Eath and Burn 2002) and coping with defeat (Carere et al. 2001, 2003; Ebner et al. 2005). Our current objective is to examine the interaction between behavioural phenotype and effects of social context during novel object exploration in a neophobic corvid species, the raven (*Corvus corax*). In both mammals and birds the presence or action (handling or food intake) of a conspecific facilitates acceptance of novel food (e.g., capuchin monkeys, *Cebus apella*: Visalberghi and Fragaszy 1995, Visalberghi and Addessi 2000, rats, *Rattus norvegicus*: Galef 1996, house mice, *Mus musculus domesticus*: Valsecchi et al. 2002, zebra finches, *Taeniopygia guttata*: Coleman and Mellgren 1994). In contrast, delay and

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Communicated by F. Bairlein.

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M. Stöwe (✉) · K. Kotrschal  
Konrad Lorenz Research Station,  
4645 Grünau 11, Austria  
e-mail: m\_stoewe@hotmail.com

K. Kotrschal  
Department for Behaviour,  
Neurobiology and Cognition, University of Vienna,  
Althanstrasse 14, 1090 Vienna, Austria

inhibition of approach to/acceptance of novel food in a social context have been observed in chum salmon, *Oncorhynchus keta* (Ryer and Olla 1991), atlantic salmon, *Salmo salar* (Brown and Laland 2001, 2002), and great tits, *Parus major* (van Oers et al. 2005). Individual differences in response to the presence of a conspecific may modulate the effect of social context on novel food or object exploration and thus could help to explain this ambiguity.

Ravens are scavengers of ephemeral food sources, for example carcasses, garbage dumps, etc. After becoming independent from their parents in their first summer, they assemble in non-breeder groups (Glutz von Blotzheim and Bauer 1993; Ratcliffe 1997). They are curious and highly exploratory but when older than 1 month post-fledging they fear almost anything new (Heinrich 1988a; 1995; Heinrich et al. 1995; Kijne and Kotrschal 2002). Conspecifics (Marzluff and Heinrich 1991), but also other bird species and mammals (e.g. wild boars, *Sus scrofa*, crows, *Corvus corone corone*, *Corvus corone cornix*: own observation, wolves, *Canis lupus*: Promberger 1992, Bugnyar and Kotrschal 2001; Stahler et al. 2002) may have facilitating effects on ravens' approach to food sources. Social context may also enhance novel object manipulation (Stöwe et al. 2006a, b).

Here we investigate whether individuals differing in behavioural phenotype are affected similarly by social context during novel object exploration. We categorize individuals as fast or slow according to their latency to approach novel objects when tested alone and compare their response to novel objects when in dyads with fast and slow conspecifics. We expect fast birds to have low approach latencies when tested in dyads with both fast and slow ravens and predict slow individuals will approach novel objects more readily when with fast conspecifics than when alone.

## Methods

### Animals and housing

In spring 2004 we hand-raised a group of 13 ravens (seven males, six females). Ravens from two nests (containing four and three ravens) were zoo-bred; birds from two other nests (containing three ravens each, one nest of three siblings and one nest with three non-siblings) were taken from the wild with permission (see "Acknowledgments"). We kept the birds in nests (for nest composition, see above) in an indoor aviary. Just before fledging we transferred all birds into one big nest in an outdoor aviary where they remained thereafter. Once fledged, we kept them together in one group with two previously raised adult males (9 and 4 years of age). Birds were marked with coloured leg-rings

for individual identification. The aviary was divided into three sections separated by wire mesh (80, 35, 80 m<sup>2</sup>) and in addition had three experimental rooms, separated by wooden walls and opaque doors. Aviaries contained trees, branches, stones, tree trunks and shallow pools for bathing. The floor was natural grass in the main compartments but gravel in the experimental rooms. Experiments were conducted in one of the large compartments (80 m<sup>2</sup>) in physical and visual, but not acoustic, isolation from the rest of the group. Birds were fully habituated to short separations from the group because this was a standard procedure in previous experiments. They were fed twice per day (in the mornings and in the afternoons after the experiments) with meat, milk products and kitchen leftovers. Water was provided ad libitum.

### Experimental set-up

We conducted novel object tests with the juveniles only, because previous experience with objects was similar for all juveniles but not for the adult birds. Two juveniles were kept in another aviary complex at the time we performed the tests, hence we tested 11 birds. From the beginning of September, when the birds were 6 months old, until the beginning of November, we tested the birds in two conditions: alone and in dyadic combinations. In the dyadic condition we combined each of 11 juveniles with every other juvenile resulting in 55 combinations (ten trials per bird). Testing order was semi-randomised: the first two ravens entering the test compartment were used as subjects unless they had been tested together before. Tests were alternated between conditions. Each bird was tested only once per day. In the dyadic tests we offered two identical novel objects (1.5 m apart) to match the number of novel objects with the number of birds in the test, to minimize competition over access to the novel objects.

In both conditions, alone and dyadic, when the bird(s) to be tested were separated the experimenter (MS) put the novel object(s) in place and observed the behaviour of the subject(s) for 20 min. The novel objects were positioned in the centre of the aviary compartment to enable the birds to approach the novel objects from all sides. Because of structures in the aviary (stones, tree trunks), the central part of the aviary compartment was not fully visible from outside. Hence, under all conditions MS took the data from one position inside the aviary. All birds were well habituated to people, including the experimenter, collecting data inside the aviary, because this had been a standard procedure for data collection since the birds fledged. It is, therefore, unlikely that the experimenters' presence in the aviary affected the ravens' approach to the novel objects.

In total, we offered four different objects in the alone condition and 15 in the pair condition (bottles, boxes, soft

toys, gloves, shoes, cups, etc., in the size range 25–45 cm). We tested all individuals with the same novel objects, but each object was presented only once per bird and the sequence was the same for all birds.

#### Data collection

For each individual we measured approach latency (in s, distance to the novel object <1 m), approach frequency and time spent close (<1 m) to the novel object (in s) and the duration of novel object manipulation (in s).

We used the duration two birds sat close to each other (distance between the birds < 50 cm) during the 20-min test period to define the quality of their social relationship. Because agonistic interactions were rare during the novel object tests, we used the dominance rank calculated on the basis of approach–retreat interactions observed during daily protocols in the same period as we conducted the novel object tests. All but one male outranked all females (Loretto et al. 2005).

#### Analysis

Because individuals did not always approach or manipulate the novel objects during the 20 min test period, we calculated latency scores instead of using exact latency times. This way we avoided cutting the distribution of latency times at the upper end (by accepting 20 min when the individuals did not approach the novel objects). The number of trials with approach was divided by the sum of latencies of all the trials (=sum of latency times when the birds approached plus 20 min for each trial the birds did not approach; Theobald and Goupillot 1990). We distinguished between slow and fast birds according to their approach latency score in the alone condition: individuals were classified as fast or slow if they approached the novel objects quicker or slower than the median of the group. When comparing the exploratory behaviour of fast and slow birds in dyadic combinations with siblings and non-siblings, calculating latency scores was not feasible, because the number of siblings differed between individuals and therefore, the number of trials with potential approach to the novel objects (which is used as a correction factor, see above) was not the same for all individuals. Instead, we calculated mean latencies. Whenever birds did not approach the novel object, we scored 20 min as latency. Because males were higher ranking than the females we statistically controlled for the effect of sex, when examining effects of rank.

Data were analysed using the software package SPSS (Version 11.0.1 2001; partial correlation coefficients) or calculated by hand, using the method described by Siegel and Castellan (1988). Only non-parametric tests were

used. Test results are given two-tailed.  $0.1 > \alpha > 0.05$  were considered as trends. Because time spent close to the novel objects correlated with the duration of novel object manipulation (Spearman rank-order correlation:  $N = 11$ , alone condition:  $r_s = 0.94$ ,  $P < 0.001$ , dyadic condition:  $r_s = 0.82$ ,  $P < 0.005$ ), we report results for time spent close, only. Birds tended to approach the novel objects with lower latencies when in sibling dyads than when in non-sibling dyads (Wilcoxon signed-ranks test:  $N = 10$ ,  $T^+ = 45$ ,  $P = 0.089$ ). Therefore, we analysed the exploratory behaviour of fast and slow birds when in combination with siblings and non-siblings separately. The time birds spent close to novel objects, in contrast, did not differ between sibling and non-sibling dyads (Wilcoxon signed-ranks test:  $T^+ = 35$ ,  $N = 10$ ,  $P = 0.49$ ). Hence, we did not distinguish between sibling and non-sibling combinations when comparing the time fast and slow individuals spent close to novel objects.

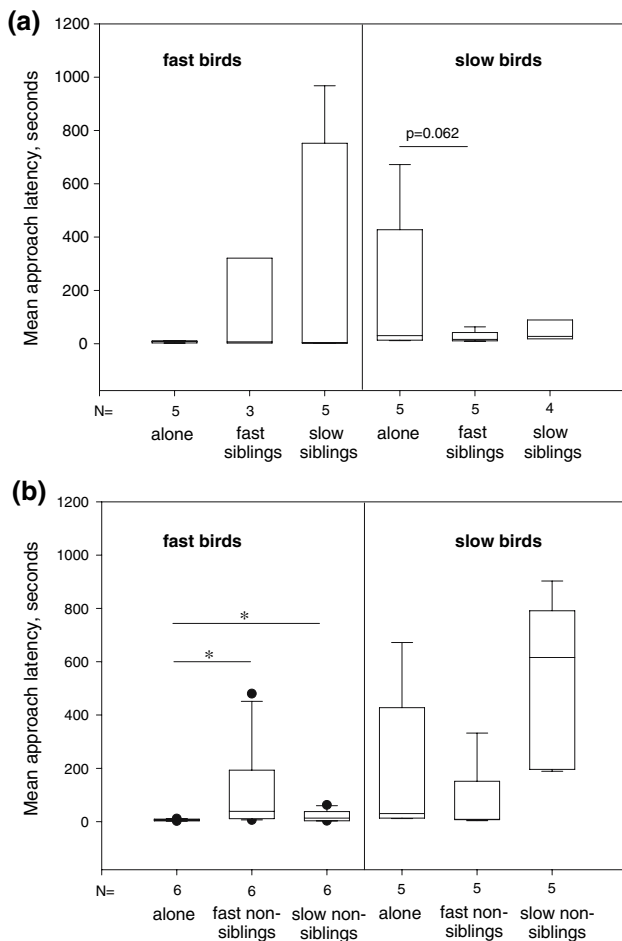
#### Results

Six individuals (four males, two females) were categorized as fast, five birds (two males, three females) as slow, according to their approach latency in the alone condition. None of the nests contained only fast or only slow individuals. We did not observe significant differences between the sexes in approach latency (Mann–Whitney  $U$  test:  $N_{1\text{females}} = 5$ ,  $N_{2\text{males}} = 6$ ,  $W_x = 24.5$ ,  $W_y = 41.5$ ,  $P = 0.34$ ) nor did social rank correlate with approach behaviour ( $N = 11$ : latency to approach: partial correlation coefficient =  $-0.23$ ,  $df = 8$ ,  $P = 0.95$ ).

The presence of siblings (Fig. 1a) and non-siblings (Fig. 1b) affected fast and slow birds differently with regard to their latency to approach novel objects (Table 1).

Fast birds did not differ in the time they spent close to novel objects when tested alone or when in dyads with fast or slow individuals (Wilcoxon signed-ranks test: alone, fast individuals:  $N = 6$ ,  $T^+ = 13$ ,  $P = 0.68$ , alone, slow individuals:  $N = 6$ ,  $T^+ = 17$ ,  $P = 0.21$ ). Slow birds, in contrast, tended to spend more time close to novel objects when in dyads with fast birds than when tested alone (Wilcoxon signed-ranks test:  $N = 5$ ,  $T^+ = 15$ ,  $P = 0.062$ , which is the lowest possible with  $N = 5$  in a two-tailed test). When in combination with slow birds they did not stay longer close to novel objects than when alone (Wilcoxon signed-ranks test:  $N = 5$ ,  $T^+ = 14$ ,  $P = 0.13$ ).

Siblings spent more time sitting close to each other than did non-siblings (Wilcoxon signed-ranks test:  $T^+ = 51$ ,  $N = 10$ ,  $P = 0.014$ ). However, we did not observe any difference between fast and slow individuals when comparing the time they spent sitting close to siblings (Mann–Whitney  $U$  test:  $N_{1\text{fast}} = 5$ , one fast bird had no siblings in



**Fig. 1** Approach latencies to the novel objects when individuals were tested alone and in dyadic combination with siblings (a) and non-siblings (b). The number of individuals ( $N$ ) varies between the tests because individuals had a different number of fast and slow siblings. Box plots show the median and the interquartile range from the 25th to the 75th percentile. Whiskers indicate the 10th and the 90th percentiles. Dots show outliers. Asterisks mark results of the Wilcoxon signed-ranks test ( $*P < 0.05$ )

the same aviary complex,  $N_{2\text{slow}} = 5$ ,  $W_x = 23$ ,  $W_y = 33$ ,  $P = 0.31$ ) or non-siblings (Mann–Whitney  $U$  test:  $N_{1\text{fast}} = 6$ ,  $N_{2\text{slow}} = 5$ ,  $W_x = 36$ ,  $W_y = 30$ ,  $P = 0.33$ ). Agonistic

interactions were rare during the tests (55 threats in 55 trials, most of which occurred during the first 4 min). Fast birds were aggressors in these interactions significantly more often than slow birds (Mann–Whitney  $U$  test:  $N_{1\text{fast}} = 6$ ,  $N_{2\text{slow}} = 5$ ,  $W_x = 46$ ,  $W_y = 20$ ,  $P = 0.0086$ ).

## Discussion

Social context indeed affected fast and slow individuals differently. Fast birds showed significantly lower latencies to approach novel objects when alone than when in dyadic combinations with non-siblings. Slow individuals, in contrast, tended to explore novel objects with lower latencies and for longer when with fast siblings than when alone. This parallels results for great tits; in these birds social context also affected fast and slow individuals differently. Slow males were more responsive to the conspecific's activity than fast males (van Oers et al. 2005): the latency to feed after a startle test was reduced with increasing activity of the accompanying bird. Fast great tits in contrast, seemed to remain unaffected by the presence of another bird. In our study also the fast individuals were affected by the presence of a conspecific but in the opposite way to slow birds. In a food-finding task fast great tits used social information to find food and responded to the behaviour of the conspecific more strongly than slow birds did. Fast birds increased their visits to feeders indicated by a tutor bird whereas slow birds did not (Marchetti and Drent 2000). Although we cannot quantify how much attention ravens paid to the conspecifics' behaviour, fast birds' waiting for the companion's response to the novel objects could be a possible explanation of their delayed approach in the dyadic condition compared with when alone. Because fast ravens approached the novel objects within  $\bar{X} = 6 + 4$  seconds when tested alone, they may easily show higher latencies if paying attention to the conspecifics' activity when tested in dyads.

As observed in several studies with mammals (Koolhaas et al. 1999) and birds (Verbeek et al. 1996), in the ravens

**Table 1** Comparison of latencies to approach the novel objects when individuals were tested alone and in dyadic combination with siblings and non-siblings

Alone condition	Dyadic condition			
	With fast siblings	With slow siblings	With fast non-siblings	With slow non-siblings
Fast birds	$N = 3$ , $T^+ = 3$ , $P > 0.99$	$N = 5$ , $T^+ = 10$ , $P = 0.62$	$N = 6$ , $T^+ = 21$ , $P = 0.031$ alone < dyads	$N = 6$ , $T^+ = 21$ , $P = 0.031$ alone < dyads
Slow birds	$N = 5$ , $T^+ = 15$ , $P = 0.062$ alone > dyads	$N = 4$ , $T^+ = 5$ , $P > 0.99$	$N = 5$ , $T^+ = 10$ , $P = 0.62$	$N = 5$ , $T^+ = 13$ , $P = 0.19$

We compared approach latencies (in seconds) of fast and low individuals using the Wilcoxon signed ranks test. The number of individuals ( $N$ ) varies between the tests because individuals had a different number of fast and slow siblings

also fast birds were more often aggressors in threat–retreat interactions than were slow birds. This indicates that the observed differences in the ravens’ approach latencies during novel object exploration are indeed related to behavioural phenotypes.

Slow birds’ approach to novel objects was facilitated when with siblings. At the time we conducted the novel object tests, young free-ranging ravens would have joined non-breeder groups after becoming independent from their parents. Sibling bonds seem to persist after independence. After 1 year our ravens still interacted significantly more often socio-positively with siblings than with non-siblings (Loretto et al. 2005), even though we had kept all the birds in one group since they fledged. Webb (2001) observed that free-ranging juvenile ravens spent significantly more time close to their siblings than to non-siblings. Advantages of these sibling bonds seem to range from support in and after agonistic interactions (Emery et al. 2003, Loretto and Bugnyar unpublished results) to facilitation during exploration (Stöwe et al. 2006a). Because scavenging ravens frequently encounter novel situations and novel food sources (Heinrich 1988b), any facilitation while searching for food is potentially advantageous, especially for young, inexperienced birds. Even if fast birds approached the novel objects more quickly when alone, they still may profit from being in a group, for example because of the risk-dilution effect (Krause and Ruxton 2002) or because of overcoming the defence of food by territory holders, other ravens (Heinrich and Marzluff 1995).

Whether social context had facilitating or delaying effects depended on the individuals’ approach behaviour and the relatedness/social relationship among the companions. Differences between the responses of fast and slow individuals to the presence of a conspecific may help to explain contradictory results from previous studies on the facilitating and inhibiting effects of social context.

**Acknowledgments** We acknowledge financial support by the FWF (P 16939 B03). 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. Sömmer for the supplying raven nestlings. Raven nestlings from the wild were taken with permit by the Ministerium für Landwirtschaft, Umweltschutz und Raumordnung des Landes Brandenburg on 25 February 2004. All experiments comply with current Austrian laws.

## References

- Armitage BA (1986) Individuality, social behaviour and reproductive success in yellow-bellied marmots. *Ecology* 67:1186–1193
- Benus RF (2001) Coping in female mice from lines bidirectionally selected for male aggression. *Behaviour* 138:997–1008
- Benus RF, den Daas S, Koolhaas JM, van Oortmerssen GA (1990) Routine formation and flexibility in social and non-social behaviour of aggressive and non-aggressive male mice. *Behaviour* 112:176–193
- Both C, Dingemanse NJ, Drent PJ, Tinbergen JM (2005) Pairs of extreme avian personalities have highest reproductive success. *J Anim Ecol* 74:667–674
- 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, Kotschal K (2001) Movement coordination and signalling in ravens (*Corvus corax*): an experimental field study. *Acta Ethol* 3:101–109
- Carere C, Welink D, Drent PJ, Koolhaas JM, Groothuis TGG (2001) Effects of social defeat in a territorial bird (*Parus major*) selected for different coping styles. *Physiol Behav* 73:427–433
- Carere C, Groothuis TGG, Möstl E, Dann S, Koolhaas JM (2003) Fecal corticosteroids in a territorial bird selected for different personalities: daily rhythm and the response to social stress. *Horm Behav* 43:540–548
- Cavigelli SA, McClintock MK (2003) Fear of novelty in infant rats predicts adult corticosterone dynamics and an early death. *PNAS* 100 26:16131–16136
- Coleman SL, Mellgren RL (1994) Neophobia when feeding alone or in flocks in zebra finches, *Taeniopygia guttata*. *Anim Behav* 48:903–907
- Daisley JN, Bromundt V, Möstl E, Kotschal K (2004) Enhanced yolk testosterone influences phenotype independent of sex in Japanese quail chicks *Coturnix japonica*. *Horm Behav* 47:185–194
- D’Eath RB, Burn CC (2002) Individual differences in behaviour: a test of “coping style” does not predict resident intruder aggressiveness in pigs. *Behaviour* 139:1175–1194
- Dingemanse NJ, de Goede P (2004) The relation between dominance and exploratory behaviour is context-dependent in wild great tits. *Behav Ecol* 15(6):1023–1030
- Dingemanse NJ, Both C, Drent PJ, van Oers K, van Noordwijk AJ (2002) Repeatability and heritability of exploratory behaviour in great tits from the wild. *Anim Behav* 64:929–937
- Dingemanse NJ, Both C, van Noordwijk AJ, Rutten AL, Drent PJ (2003) Natal dispersal and personalities in great tits (*Parus major*). *Proc R Soc Lond B* 270:741–747
- Dingemanse NJ, Both C, Drent PJ, Tinbergen JM (2004) Fitness consequences of avian personalities in a fluctuating environment. *Proc R Soc Lond B* 271:847–852
- Drent PJ, van Oers K, van Noordwijk AJ (2003) Realised heritability of personalities in the great tit (*Parus major*). *Proc R Soc Lond B* 270:45–51
- Ebner K, Wotjak CT, Landgraf R, Engelmann M (2005) Neuroendocrine and behavioural response to social confrontation: residents versus intruders, active versus passive coping styles. *Horm Behav* 47:14–21
- Emery NJ, Seed AM, Clayton NS (2003) Alliance formation and social complexity in rooks (*Corvus frugilegus*). *Revista de Etologia Suppl* 5:59
- Galef BG Jr (1996) Social enhancement of food preferences in Norway rats: a brief review. In: Heyes CM, Galef BG Jr (eds) *Social learning in animals, the roots of culture*, Academic, San Diego, pp 49–64
- Glutz von Blotzheim UN and Bauer KM (1993) *Handbuch der Vögel Mitteleuropas*. Band 13/III, Passeriformes (4.Teil.), Aula/Wiesbaden, pp 2018
- Gómez-Laplaza LM (2002) Social status and investigatory behaviour in the angelfish (*Pterophyllum scalare*). *Behaviour* 139:1469–1490
- Gosling SD, John OP (1999) Personality dimensions in nonhuman animals: A cross-species review. *Curr Dir Psychol Sci* 8:69–75

- Groothuis TGG, Carere C (2005) Avian personalities: characterization and epigenesis. *Neurosci Biobehav Rev* 29:137–150
- Heinrich B (1988a) Why do ravens fear their food? *The 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 (1995) Neophilia and exploration in juvenile common ravens, *Corvus corax*. *Anim Behav* 50:695–704
- Heinrich B, Marzluff JM (1995) Why ravens share? *Am Sci* 83:342–350
- Heinrich B, Marzluff JM, Adams W (1995) Fear and food recognition in naive common ravens. *Auk* 112:499–503
- Kijne M, Kotschal K (2002) Neophobia affects choice of food item size in group foraging common ravens (*Corvus corax*). *Acta Ethol* 5:13–18
- Koolhaas JM, Korte SM, de Boer SF, van der Vegt BJ, van Reenen CG, Hopster H, de Jong IC, Ruis MAW, Blokhuis JH (1999) Coping styles in animals: current status in behaviour and stress-physiology. *Neurosci Biobehav Rev* 23:925–935
- Kralj-Fišer S, Scheiber IBR, Blejec A, Kotschal K (2007) Do personalities show in free-roaming greylag geese? A test of behavioural and physiological consistency over time and across situations. *Horm Behav* 51:239–248
- Krause J, Ruxton GD (2002) *Living in groups*. Oxford University Press, Oxford
- Loretto M-C, Kotschal K, Bugnyar T (2005) Ontogeny of dominance relations of juvenile common ravens (*Corvus corax*). XXIX International Ethology Conference, 20–27 August, Budapest, pp 136
- Marchetti C, Drent PJ (2000) Individual differences in the use of social information in foraging by captive great tits. *Anim Behav* 60:131–140
- Marzluff JM, 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
- van Oers K, Drent PJ, de Goede P, van Noordwijk AJ (2004) Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proc Roy Soc Lond B* 271:65–73
- van Oers K, Klunder M, Drent PJ (2005) Context dependence of personalities: risk-taking behaviour in a social and non-social situation. *Behav Ecol* 16:716–723
- van Oers K, Drent PJ, Kempenaers B (2006) Personality and promiscuity in the Great Tit. *J Ornithol* 147(Suppl):7
- Promberger C (1992) Mitteilungen aus der Wildforschung: Wölfe und Raben im Yukon. *Der Oberösterreichische Jäger* 56:34–35
- Ratcliffe D (1997) *The raven*. Academic, San Diego
- Ryer CH, Olla BL (1991) Information transfer and the facilitation and inhibition of feeding in a schooling fish. *Environ Biol Fishes* 3:317–323
- Siegel S, Castellan NJ 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
- SPSS (2001) *SPSS for windows*, Version 11.0.1, SPSS, Chicago
- 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 MC, Schloegl C, Range F, Kotschal K (2006a) Novel object exploration in ravens (*Corvus corax*): effects of social relationships. *Behav Proc* 73:68–75
- Stöwe M, Bugnyar T, Heinrich B, Kotschal K (2006b) Effects of group size on approach to novel objects in ravens (*Corvus corax*). *Ethology* 112:1079–1088
- Theobald CM, Goupillot RP (1990) The analysis of repeated latency measures in behavioural studies. *Anim Behav* 40:484–490
- Valsecchi P, Bosellini H, Sabatini F, Mainardi M, Fiorito G (2002) Behavioural analysis of social effects on problem-solving ability in the house mouse. *Ethology* 108:1115–1134
- Verbeek MEM, Bonn A, Drent P (1996) Exploration, aggressive behaviour and dominance in pair-wise confrontations of juvenile male great tits. *Behaviour* 133:945–963
- Visalberghi E, Fragaszy D (1995) The behaviour of capuchin monkeys, *Cebus apella*, with novel food: the role of social context. *Anim Behav* 49:1089–1095
- Visalberghi E, Addessi E (2000) Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Anim Behav* 60:69–76
- Webb WC (2001) Common raven juvenile survival and movements in a human-augmented landscape. Master's thesis. University of California, Riverside