Foraging innovations and kleptoparasitism in birds

Julie Morand-Ferron
Department of Biology
McGill University, Montreal

January 2007

A thesis submitted to McGill University
in partial fulfilment of the requirements of the degree of
Doctor of Philosophy

Library and
Archives Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 978-0-494-32219-2
Our file Notre référence
ISBN: 978-0-494-32219-2

NOTICE:
The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distribute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:
L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Abstract

The ability to invent new solutions to old or novel problems is often equated with intelligence, both in humans and non-human animals. Behavioural flexibility can be defined operationally by looking at the frequency of novel or unusual behaviours, i.e. innovations, in different taxa. Despite the potential survival benefits of behavioural flexibility in the face of changing conditions, there is variation among taxa in the propensity to innovate. Here, I examine in detail one foraging innovation, dunking behaviour (the immersion of food items in water) in Carib grackles (*Quiscalus lugubris*) of Barbados. I show that the rarity of dunking behaviour in the field is not due to the inability of most individuals to learn and/or perform it, but rather to the balance of costs and benefits not being favourable to its expression in most field conditions. In this population, dunking functions as a proto-tool food-processing technique speeding the ingestion of items that are difficult to swallow. The frequency of the behaviour depends on food characteristics, travel costs between the food source and water, and the probability of losing items to conspecifics. Dunking renders grackles vulnerable to food theft because it involves releasing food items in water, where there is often a build-up of conspecifics. When faced with a high risk of kleptoparasitism, grackles reduce the frequency of dunking, engage in aggressive displays, and keep items in the bill while dunking. Kleptoparasitism not only reduces the rate of dunking by increasing costs to the behaviour, but also by constituting an alternative foraging tactic. The payoffs to this tactic are frequency-dependent; i.e. they decrease as the frequency of kleptoparasites increases in the group. A comparative study on ecological, morphological and behavioural predictors of the occurrence of kleptoparasitic tactics among bird families point to an important role of predation and cognitive abilities in favouring the evolution of kleptoparasitism. Thus, avian food-stealing should not be regarded as a "cognitively simpler" alternative to intelligent behaviour, but as another form of behavioural flexibility. Large-brained primates and birds share the ability to learn quickly, innovate, use tools and engage in exploitative tactics, suggesting that these abilities have not been traded-off against each other, but have instead evolved together.

Résumé

La capacité de résoudre les problèmes en inventant de nouvelles solutions est considérée comme une marque d'intelligence chez les humains, mais aussi chez les animaux. La flexibilité comportementale peut être définie de façon opérationelle en notant la fréquence des comportements nouveaux ou inhabituels, i.e. les innovations, chez différents groupes taxonomiques. La flexiblité comportementale peut contribuer à la survie d'animaux soumis à d'importants changements environnementaux; pourtant ce ne sont pas tous les taxons qui semblent capables d'innover. Dans cette thèse, j'examine en détail une innovation alimentaire, le trempage des aliments chez le quiscale merle (*Quiscalus lugubris*) de la Barbade. En nature, la rareté du comportement de trempage n'est pas due à l'incapacité d'une partie de la population à apprendre ou exécuter le comportement, mais plutôt au fait que la balance des coûts et bénéfices est rarement favorable à son expression. Dans cette population, le trempage est une technique de proto-outil qui accélère l'ingestion des aliments difficiles à avaler. La fréquence du comportement dépend des caractéristiques des aliments, des coûts de transport des aliments jusqu'à une source d'eau ainsi que de la probabilité de cleptoparasitisme par les conspécifiques. Le trempage rend les quiscales vulnérables au cleptoparasitisme car cela implique de relâcher les items dans l'eau où il y a souvent une accumulation de conspécifiques. Lorsque confrontés à une forte probabilité de vol, les quiscales réduisent leur fréquence de trempage, font plus de parades aggressives, et maintiennent les items dans le bec en trempant. Le cleptoparasitisme ne réduit pas seulement la fréquence du trempage à cause des coûts qu'il implique, mais aussi en constituant une tactique d'alimentation alternative au sens de la théorie des jeux. Les gains associés à cette tactique d'exploitation sont fréquence-dépendants, c'est-à-dire qu'ils diminuent à mesure que la fréquence des cleptoparasites augment dans le groupe. Les résultats d'une étude comparative sur les prédicteurs écologiques, morphologiques et comportementaux du cleptoparasitisme suggèrent que l'évolution du cleptoparasitisme a été favorisé chez les familles d'oiseaux s'adonnant à la prédation et possédant de bonnes capacités cognitives. Le vol alimentaire chez les oiseaux n'est donc pas nécessairement une alternative aux comportements intelligents, mais peut être perçu comme une autre forme d'expression de la flexibilité comportementale. Les primates et les oiseaux encéphalisés partagent la capacité d'apprendre rapidement, d'innover, d'utiliser des outils et des tactiques d'exploitation sociale, ce qui suggère que ces habiletés ont évolué ensemble.

Table of Contents

List of Tables and Figures

Acknowledgements

I would like to thank my supervisor, Louis Lefebvre, for his cheerful encouragements and his generosity in explaining his views on how science should be approached and communicated. Under his expert supervision, I have not only learned an extraordinary amount of amazing facts of science, but most importantly, I have learned to think critically about science. I am also extremely grateful to Daniel Sol and Simon Reader for helping me going through my first steps as a researcher. They proved to be excellent models of rigor, creativity, and hard work. I would also like to thank Don Kramer and Luc-Alain Giraldeau for their thoughtful advice as members of my supervisory committee.

I would also like to thank other members of the department with whom I have discussed ideas and who also contributed to make my passage at McGill enriching on a human level, including Sarah Overington, Neeltje Boogert, Andrea Griffin, Denis Réale, Carolyn Hall, Henri Valles, Patrick Leighton and Katerine Turgeon. Special thanks to Mélisa Veillette who proved to be of crucial assistance in completing field observations in Barbados, and to Martin Frost, who taught me how to take morphological measurements on grackles and allowed me to discover the nicest natural spots for birdwatching in Barbados.

Very special thanks to Éric Trottier who supported me in all my professional decisions, from summer research in ornithology (this means waking up at three in the morning), to moving from Québec city to Montréal. He was even directly involved in watching grackles in Barbados and helped me out with some technical aspects of the work (e.g. the "Trottier" water puddles). Finally, I would also like to thank my parents for always reinforcing my ever-growing curiosity for everything that surrounded me. My trip towards scientific research in animal behaviour probably started on the day when my cat caught a juvenile chipmunk in the yard without hurting it badly; my parents explained to my consternation that the chipmunk's mom would probably reject the juvenile because its smell had been altered, and we fortunately managed to care for the cute creature.

Contribution of authors

Chapter 1. This chapter is based on a paper co-authored by Julie Morand-Ferron, Louis Lefebvre, Simon Reader, Daniel Sol and Sandra Elvin, published in Animal Behaviour in 2004 (vol. 68, pp. 1267-1274). Simon Reader and Louis Lefebvre first witnessed dunking behaviour in Carib grackles in Barbados. In the context of other experiments, they observed a wild grackle dunking a piece of bread in a rain puddle on a terrace at the Bellairs research Institute of McGill, and a captive grackle dunking a maraschino cherry in its bowl of water. Louis Lefebvre suggested investigating costs and benefits of dunking in the field and looking at captive grackles to see whether most of them or only a few individuals could perform the behaviour. He also did the pilot work for Experiment 1. Then, I devised and conducted the field and captive observations on grackles for Experiments 2 and 3. Sandra Elvin conducted about half of the field observations for Experiment 3. Statistical analyses were conducted with the help of Simon Reader and Daniel Sol.

Chapter 2. This chapter is based on a paper co-authored by Julie Morand-Ferron, Mélisa Veillette and Louis Lefebvre, published in Behavioural Processes in 2006 (vol. 73, pp. 342-347). I conducted field observations for Part A, and devised the field observations protocol for Part B and C, while it is Mélisa Veillette who actually videotaped the grackles in the field for these two last sections. I then gathered the data from the videorecordings and ran all statistical analyses.

Chapter 3. This chapter is based on a manuscript co-authored by Julie Morand-Ferron, Luc-Alain Giraldeau and Louis Lefebvre, to be submitted to Behavioral Ecology. I devised and conducted field experiments, and gathered data from videorecordings. Luc-Alain Giraldeau provided assistance in developing the protocol and analysing the data. Mélisa Veillette provided help with videotaping the experiments.

Chapter 4. This chapter is based on a manuscript co-authored by Julie Morand-Ferron, Daniel Sol and Louis Lefebvre, that is currently under revision in Proceedings of the Royal Society B: Biological Sciences. I reviewed the literature and electronic indexes in order to build the database on avian kleptoparasitism. I devised and ran all analyses, except for the phylogenetic reconstruction analyses (Daniel Sol).

Appendix I is based on a paper published in Wilson Bulletin in 2005 (vol.117, pp. 405-407). I am the sole author and experimenter for this paper.

Louis Lefebvre has supervised the planning of experiments, data analysis, results interpretation and writing up of articles throughout the thesis.

General Introduction: Why is intelligence rare?

As humans, we see intelligence as a desirable trait that allows us to solve problems, invent new solutions, and construct and use technology (Rogers 1993). Even if human intelligence has characteristics that are unique to the species, the idea that at least some of its features may be present in other animals has been the focus of much research ever since Romanes (1883) published observations of apparently intelligent behaviours in support for the Darwinian assumption of evolutionary continuity (Darwin 1871). Over the years, the challenge has been to develop operational definitions of intelligence that could include non-human animals and procedures that would as much as possible control for anthropomorphic biases.

Approaches to the study of animal intelligence: can a species pass the test?

A brief and non-exhaustive review of the different approaches to animal intelligence can be broadly structured according to two sets of methods: those that examine the success or failure of animal species on a specific test, and those that seek to compare animals on some quantitative criterion of intelligence. The first method involves devising experimental tasks under the assumption that success on the task is indicative of the ability of a species to engage in certain cognitive processes used by humans. For example, language is often considered to be an ability that is unique to humans (Chomsky 1972; MacPhail 1985), and many tests have been conducted in order to see whether different species, mostly primates, could develop language-related abilities. Pioneer work by Gardner & Gardner (1969) and Premack (1971) involved training chimpanzees (*Pan troglodytes*) to learn associations between words and objects (the Gardners used American sign language, while Premack used plastic symbols in conducting the tests). Further tests were then conducted on non-primates species such as bottlenose dolphins, *Tursiops truncatus* (Herman et al. 1984) and African grey parrots, *Psittacus erithacus* (Pepperberg 2002). Kaminski et al. (2004) recently showed that some dogs could learn to differentiate hundreds of different referential signals and learn new ones extremely rapidly by pairing an unknown object with an unknown word. Nevertheless, there is general agreement that some language-related abilities are unique to humans (Hauser et al. 2002).

The use of verbal language allows humans to communicate about events and objects that are remote in time or space. It has been suggested that the ability to think about past events and to project one's self into the future in imagination, or "mental time travel", is a cognitive ability that is unique to humans (Tulving 1983; Suddendorf & Busby 2003). Humans are able to remember specific events that occurred in the past through the use of episodic, as opposed to declarative, memory (Tulving 1983). Clayton and colleagues have devised tests to examine whether the ability to remember the specific contents of a memory in terms of where, when and what happened is present in food-caching birds. Western scrub jays (*Aphelocoma coerulescens*) could indeed remember what type of food they cached in a specific location and how long ago the cache had been made: the birds recovered the preferred, perishable items when they had been cached recently, but only non-perishable items when the caches had been made several days before (Clayton & Dickinson 1998). These corvids were thus said to possess an episodic-like memory. Furthermore, western scrub-jays that had experience in pilfering the caches of others would re-cache items in new locations if they have been observed by a conspecific while caching these items; in contrast, birds that were not previously given the opportunity to pilfer the caches of conspecifics would be naive to the risk of being robbed of food and would not engage in cache protection behaviours even when they had been observed while caching (Emery & Clayton 2001). The experienced birds did not learn to recache food in response to cache loss, as their caches were never actually pilfered; it seems rather that they could use their own experience as pilferers to avoid being pilfered by knowledgeable conspecifics, a possible case of "experience projection" (Emery & Clayton 2004b).

The ability to attribute mental states to others, or Theory of Mind (Premack & Woodruff 1978), has been suggested to rely on the perception of a self that can be distinguished from other individuals. The question of whether animals have a concept of self has been investigated with the mirror self-recognition test, first devised by Gallup in 1970. This test consists in placing a mark on a conspicuous body part of the animal while it is under anaesthesia, and then note the reaction of the animal when placed in front of a mirror: if the animal touches the mark in the mirror, or reacts with aggressive or other social displays normally exhibited in presence of a conspecific, the experimenter concludes that the animal has failed the test. In order to pass the test, animals have to attend to the mark on their own body, a criterion that only apes and dolphins seem to reach (Povinelli et al. 1997; Reiss & Marino 2001). In reaction to the failure of many monkeys to pass the mirror self-recognition test, but their apparent recognition of themselves as distinct individuals ("social self" but not "self-awareness"; Seyfarth & Cheney 2000), researchers have devised experiments that examine other components of Theory of Mind, such as the ability to recognise the knowledge and states of attention of others (e.g. Hare et al. 200; Hare et al. 2003; Bugnyar & Heinrich 2005).

The evolution of a Theory of Mind, and more generally of advanced cognitive abilities, is suggested to have been favoured in animals living in stable, cohesive groups (Jolly 1966; Humphrey 1976; Byrne & Whiten 1988; Call 2001). The "social complexity hypothesis" suggests that the need to recognize individuals and to remember past interactions with and between different individuals might have selected for increased memory and cognitive capacity. As not all interactions between all individuals of a group can be monitored, group-living animals might have developed the ability to infer relationships from their own restricted experience (Seyfarth & Cheney 2003). For example, seeing individual A winning an aggressive interaction over B, and B winning over C would lead to the conclusion that A is dominant to C, an ability termed "transitive inference" (Bond et al. 2003). Up to now, the use of transitive inference in social settings has been demonstrated only in pinyon jays, *Gymnorhinus cyanocephalus* (Paz-y-Mino et al. 2004).

The role of sociality in the evolution of animal intelligence has traditionally been opposed to the role of ecological (non-social) and technical factors. The classic experiments of Köhler (1927) examined the possibility that animals could solve problems by insight, the sudden reorganization of experience to find a novel solution (Thorpe 1963). Köhler (1927) observed chimpanzees piling up boxes to reach bananas with a stick and concluded that their solution of the problem showed insight. However, because the chimpanzees had previous experience with sticks and boxes, the most parsimonious explanation is that they probably arrived at the solution by trial-and-error (Emery & Clayton 2004a). A demonstration of insight learning would require that animals find a solution in only one step, using elements of the environment not encountered before (Povinelli 2000). Another test for insightful problem-solving is the string-pulling test, which is often used with birds. The test involves presenting animals with food suspended on a string that can only be obtained by pulling repeatedly at the string and tucking each pulled segment under the foot. Because pulling the string only once does not provide any reward, success by animals that have never encountered food attached on a string before is thought to require sudden understanding of the means-end connection between the food and the string, and thus insight. In a string-pulling test conducted on ravens, *Corvus corax*, most individuals first tried to jump or fly at the food, but one bird actually solved the task on the first trial, suggesting that it was capable of insightful problem-solving (Heinrich 1995). Variants of the string-pulling tasks involving different configurations of strings (i.e. crossed, parallel, etc.) are being used in evaluating what animals understand in a technical problem-solving context (Osthaus et al. 2005; Halsey et al. 2006; Werdenich & Huber 2006). Only ravens and keas (*Nestor notabilis,* a carnivorous parrot; Werdenich & Huber 2006) seem to be able to solve the string-pulling with the speed one would normally expect of insight.

The manufacture and use of tools have long been suggested to constitute a key element in the evolution of hominid intelligence (Oakley 1959; Wynn 1988; Boesch 1996). Extensive observations of wild animals have now revealed many cases of tool use in the field, ranging from termite-fishing in chimpanzee to stick probing in finches (for a review, see Beck 1980). Many tests have been devised in order to see whether animals could manufacture and use tools, and when they succeeded, what they understood about the task. A classic technique is the trap-tube test, devised by Visalberghi & Limongelli (1994), which consists in placing a food reward in a transparent tube in which a hole has been practised; the animal has to push or pull out the reward with a stick in a manner that will prevent the food from falling in the trap. The observer examines whether animals understand the physical connection between the trap and the loss of the reward. Variants of this task have been devised for a variety of primate and bird species, with different levels of difficulty and different ways of accommodating the particular motor behaviour of different taxa (e.g. pushing is thought to be easier than pulling for primates, which succeed better when confronted with an apparatus requiring pushing the reward out of the tube; Mulcahy & Call 2006).

Over all the tests described above, the taxonomic distribution of success seems to show two clear patterns: (1) few animals can solve these tests, and intelligence thus seems to be rare, and (2) most animals that solve these tests have the largest brains of their class or order, i.e. apes, odontocetes, corvids and parrots. For example, anthropoid apes, but not monkeys, pass the mirror self-recognition test (de Waal et al. 2005). Recent years have shown a diversification in the range of species tested, with surprising results coming from avian studies of intelligence (reviewed in Emery 2006). For example, direct evidence for episodic-like memory has been obtained only in western scrub jays (but see criticism in Suddendorf & Busby 2003); primates do possess "what-where" memories, but do not seem to remember how long ago a certain event has occurred and thus do not encode a "when" component (De Kort et al. 2005).

Another realisation is that many behaviours previously thought to be based on complex cognitive processes have now been attributed to simpler, lower-level mechanisms. In many cases, the action of simple cognitive processes such as associative learning directed towards rewarding objects through learning constraints can result in remarkable feats of animal behaviour (Gould 2004). For example, some proficient tool-using animals such as capuchin monkeys (*Cebus apella*) and woodpecker finches (*Cactospiza pallida*) do not appear to understand means-end relationships between elements of tool-related tasks. Instead, they rely on trial-and-error learning and the use of procedural rules (Visalberghi & Limongelli 1994; Tebbich & Bshary 2004). Moreover, New Caledonian crows (*Corvus moneduloides*) and woodpecker finches can develop tool-use behaviours individually by directed trial and error. They spontaneously manipulate tools with no prior experience and do not require social learning in order to develop functional tool-using abilities (Tebbich et al. 2001; Kenward et al. 2005). However, tool-users can exhibit a high degree of *flexibility* in tool-related behaviours (Sakura & Matsuzawa 1991; Bermejo & Illera 1999; Chappell & Kacelnik 2002). The correlation of tool-related behaviours with a large residual brain size in birds (Lefebvre et al. 2002) and primates (Reader & Laland 2002) also suggests that tool-use might nevertheless be cognitively-demanding and used as an operational definition of intelligence.

Quantitative variation in animal intelligence

The second method for the study of animal intelligence seeks to compare different taxa on some quantitative criterion. At least four traditions have used this approach: comparative psychology of learning, comparative biology of ecological correlates, neuroecology of restricted adaptive specializations, and comparative analyses of behavioural flexibility. Comparative psychologists have looked at the relative performance of different animal species on various learning tests in controlled laboratory conditions. By confronting animals with artificial tasks, they target general-purpose intelligence at solving novel problems. For example, Bitterman (1965) compared the number of errors made on a reversal learning task by African mouthbreeders and rats, showing that rats would learn very quickly after a few trials while fish never seem to improve. Gossette (1968) extended such a comparison to seven mammalian and ten avian species, and suggested that there were indeed species differences in the number of errors made at reversal learning tasks. Riddell & Corl (1977) found strong correlations between cerebral indices, including Jerison's (1973) EQ index, and the learning performance of 23 species on different tasks. The advantage with the experimental method is that it allows controls and tests of mechanisms. However, critics of this approach saw the process of ranking animals on a continuous phylogenetic scale as an outdated *scala naturae* conception of evolution (Hodos & Campbell 1969; see also comments in MacPhail 1987). Furthermore, despite suggestions on ways to reduce biases favouring some species over others (Bitterman 1965), differences in perception and motor skills can always be invoked to explain difference in performance among the species, making the null hypothesis of no difference in learning abilities between the different species almost impossible to reject (Macphail 1987; Pearce 1997).

An alternative approach that emphasizes the need to look at ecologically-relevant challenges faced by animals is that of comparative biology. This approach tests predictions on the relationship between brain size and ecological problems that are assumed to be cognitively-demanding. Starting with the work of Clutton-Brock & Harvey (1980), comparative biologists have thus been able to conduct large-scale studies on a wide variety of both social and ecological predictors of intelligence: feeding ecology (Harvey et al. 1980; Bennett & Harvey 1985b) habitat use (Barton 1996), parental care (Gittleman 1994), mate attraction (Madden 2001; Devoogd et al. 1993), social complexity and group size (Kudo & Dunbar 2001; Burish et al. 2004). In all cases, the prediction is that animals with lifestyle A should on average have larger brains than do animals with a lifestyle B, based on the assumption that lifestyle A is more cognitively-demanding than lifestyle B. For example, living in larger social groups is assumed to select for improved information-processing capacities, and thus a bigger brain, because of the increased demands of recognising individuals, remembering past interactions and dealing with a large pool of competitors (Barton 1996). However, these assumptions have not always been addressed empirically, and results may vary depending on which exact operational definition is used. In addition, the actual cognitive abilities thought to be the link between the demands of a particular lifestyle and brain evolution are never directly measured.

Starting in the early 80's, the modular neuroecology approach sought to understand the intelligence of animals in their own niche, by looking at the relationship between the size of the neural substrate for a *specific* behaviour and behavioural performance in laboratory tests using a set of closely related species. The focus of neuroecology is not on what is shared by the different species in terms of intelligence, as in the comparative psychology of learning approach, but on species-specific adaptations to a particular ecological challenge, i.e. adaptive specialisations (Shettleworth 1998). As explained by Kamil (1988), this approach is integrative: instead of looking at the two-way association between the brain and behavioural performance (i.e. comparative psychology) or between the brain and ecology (i.e. comparative biology), neuroecology seeks to link brain, behaviour and ecology in an evolutionary framework. One of the most discussed example of adaptive specialisation concerns food-storing in corvids and parids. The basic predictions of the neuroecological approach on food-storing are that animals with a greater ecological reliance on cached food (1) should perform better in tests of spatial memory (2) and have a larger neural substrate for spatial memory, the hippocampus (Krebs et al. 1989), than animals that are not or less dependent on stored food. In a recent re-analysis of data available on corvids and parids, Lucas et al. (2004) found a correlation between the degree of caching specialization and hippocampal size within each of these two families, thereby providing support for the second prediction (see also Garamszegi & Eens 2004). Comparative tests of food retrieval ability have shown that storing species most often perform better than non-storers on a variety of spatial tasks, but the difference was sometimes much smaller than expected (e.g. Krebs et al. 1990) or in some cases went against predictions (Macphail & Bolhuis 2001). A better understanding of selection pressures might lead to a refinement of the assumptions made in drawing predictions; for example, non-storers might not be expected to be poor in all spatial memory tasks, only those that require remembering locations for a long time (Healy et al. 2005). If laboratory tests of spatial memory tap into both general purpose learning and specialised learning and if the two are traded-off (good storers are poor innovators and vice-versa; Lefebvre & Bolhuis 2003), this alone might prevent the predicted differences from coming out clearly in many experiments.

Further work in modular neuroecology of spatial memory and the hippocampus has also addressed sex differences in brood-parasitic cowbirds (Sherry et al. 1993; Reboreda et al. 1996) and adaptive specialisation brought about by intrasexual competition for mating opportunities in voles (*Microtus*). Males from polygynous vole species have a larger home range, perform better in tests of spatial memory, and have a larger hippocampus than females, while these differences are not found in monogamous species (reviewed in Sherry 2006). Work on the neuroecology of birdsong by DeVoogd and colleagues (1993; Szekely et al. 1996) have revealed that song repertoire size correlates with HVC volume, a brain nucleus involved in song learning and production (Nottebohm 1981).

Niche-specific minds or behaviourally flexible animals

A fourth approach has recently examined direct (contrary to comparative biology) operational measures of unspecialised cognition (contrary to modular neuroecology) in the wild (contrary to comparative psychology). The comparative analysis of behavioural flexibility (Lefebvre et al. 1997, 2004; Reader & Laland 2002; Sol et al. 2005a, 2005b, 2005c) emphasizes the observation of wild animals confronted with ecologically relevant problems. By comparing animals on their ability to invent new solutions to ecological and social challenges, it is focusing on general intelligence of animals expressed spontaneously in the field.

The modular neuroecology approach suggests that natural selection can act to create niche-specific minds designed to solve particular ecological challenges (Shettleworth 1998). Because neural tissue is metabolically expensive, modular neuroecologists expect that adaptive specialisations in one domain will have to be traded-off against neural tissue, and thus, behavioural abilities in other domains (Sherry & Schacter 1987). The idea that selective pressures on certain behavioural capacities can lead to the specific enlargement of the neural substrate for this behaviour independent of changes in other parts of the brain has found some support in accounts of mosaïc (de Winter & Oxnard 2001), rather than concerted (Finlay & Darlington 1995), evolution of the brain. The negative correlation between reliance on food-hoarding and innovativeness is suggested to exemplify such a trade-off (Lefebvre & Bolhuis 2003). However, other behavioural abilities, such as learning speed, tool-use frequency, and innovation frequency have been shown to correlate positively among birds and primates (reviewed in Lefebvre et al. 2004). These positive correlations suggest that some abilities are not traded-off against each other; instead they may have evolved together, or they may be different expressions of what comparative psychologists call general intelligence.

While recurring ecological problems across generations favour the evolution of genetically-determined solutions or innate predispositions to interact with certain parts of the environment or learn certain behaviours, important changes in conditions between generations will prevent these specialisations from being stabilized over evolutionary time (Stephens 1991; Kerr & Feldman 2003). Such highly variable environments will be tracked more efficiently by animals endowed with the ability to adjust their behaviour to prevailing conditions and to learn quickly, provided that the value of at least some important predictors of food, mates, or predators remain constant within the lifetime of these animals (Stephens 1991). Some environments might thus select for the ability to take advantage of regularities (e.g. associative learning, cultural transmission) while being able to switch between many different behavioural solutions when faced with changes (e.g. innovation, opportunism) – i.e. a specialisation on behavioural flexibility.

An operational measure of behavioural flexibility

Although the importance of behavioural flexibility in influencing the evolution of animals in their environment has often been discussed (Wyles et al. 1983; Sol et al. 2005c; Phillimore et al. 2006) it has proved difficult to define operationally. In ecology, many definitions have been proposed: number of motor patterns used (Klopfer 1967), number of food types eaten (Sherry 1990; Owens et al. 1999), number of foraging strategies used (Ratcliffe et al. 2006), etc. The specialist-generalist continuum has also been used as a way to classify taxa according to their level of flexibility in exploiting resources from the environment. However, it has been found that some generalists populations are composed of specialised individuals (Fox & Morrow 1981; Werner & Sherry 1987; Scott et al. 2003) and that some individuals or taxa behaving like specialists are capable of behavioural flexibility when some constraints are removed (Alatalo et al. 1985). Moreover, one general difficulty with these definitions of behavioural flexibility is to find a criterion of classification that will suit different taxa. For example, one can use the number of modes of hunting within solitary felids, but this would not be comparable with modes used by group-hunting canids. Lefebvre and colleagues (1997; 2004) have proposed using novel or unusual behaviours, i.e. innovations, exhibited by wild animals as an operational measure of behavioural flexibility. This measure considers the set of well-known species-typical behaviour patterns as a baseline and looks only at departures from this set. For example, a heron standing in shallow water and seizing fish with its bill would not be deemed innovative, as this behaviour is part of typical heron behaviour. However, a common myna (*Acridotheres tristis*) engaging in the same behaviour is considered innovative as this behaviour is not reported to occur in this species (Davidar 1991).

The advantages of this method for quantifying behavioural flexibility is that (1) it is based on spontaneous behaviour by the animal in the field (compared with tasks completed by animals in captive settings where they have no other option than attempting to solve the task), (2) it is available for hundreds of avian and primate species as a result of the collective effort of ornithologists and primatologists, and (3) the criterion for flexibility does not depend on any subjective evaluation of cognitive processes involved in the behaviour, but the simple observation that the behaviour has not been reported before. However, the main drawback is that the judgment as to whether a behaviour is indeed a novel behaviour in the species depends on previous knowledge accumulated on the species, which itself depends on research effort on the taxa. One way of circumventing this is to record novel behaviours in well-studied taxa, or in monitored populations. For example, one of the most famous cases of foraging innovations is the invention of sweet potato-washing in Japanese macaques (*Macaca fuscata*; Kawai 1965). This particular case complies with Reader & Laland's (2003) criterion to identify innovations: it is a novel, learned behaviour that was then integrated in the population's repertoire. Because this innovation occurred in a monitored population, researchers could insure that the behaviour was indeed novel; it was also not merely accidental, as it was then integrated in the behavioural repertoire of the inventor. The researchers could thus date the first occurrence of the behaviour, identify its inventor and the route of cultural transmission of the innovation within the group. However, monitored populations are few, and it might often be useful to adopt a less restrictive operational definition (Reader & Laland 2003). Recording the occurrence of innovations as departures from the species-typical repertoire in taxa for which natural history is reasonably well-known can lead to a useful quantification of behavioural flexibility, after taking into account research effort (van Schaik et al. 2006; Lefebvre et al. 2004).

Using the frequency distribution of reports of innovative foraging behaviour (i.e. the ingestion of a new food type or the invention of a novel foraging technique) collected from the short notes section of dozens of ornithological journals, Lefebvre et al. (1997) showed that innovation rate was correlated with the relative size of the forebrain in birds. This relationship was tested for the effect of nine confounding variables, including juvenile development mode, observer bias, research effort and phylogeny (Lefebvre et al. 1998; Nicolakakis & Lefebvre 2000). The best neural correlate of innovation rate in birds is the residual size of the mesopallium (Timmermans et al. 2000), a telencephalic region involved in higher cognitive processes such as the integration of information from different modalities (Reiner et al. 2005). Reader & Laland (2002) have shown that innovativeness is positively correlated with the residual size of the neocortex in primates, drawing a striking parallel with results obtained on birds. Innovation rate thus appears to be a useful measure of behavioural flexibility taken from the field (Seyfarth & Cheney 2002; Marino 2005; Sherry 2006).

Costs and benefits of innovativeness

Cases studies have demonstrated the crucial role of behavioural flexibility in avoiding novel predators (Berger et al. 2001), exploiting prey with variable population densities (Estes et al. 1998) or reducing rates of expression of a behaviour when costs suddenly outweigh benefits (Brooke et al. 1998). Observations of specific innovations in the wild have provided evidence that behavioural flexibility can contribute to survival in the face of important environmental change (Boag & Grant 1981) and may also allow the successful exploitation of a vacant ecological niche (Terkel 1995). The comparative analysis of behavioural flexibility allows an examination of long-standing predictions from the ecological literature, and thereby provides a test of the generality of these observations. Comparative work by Sol and colleagues (2005a) revealed that innovative birds survive better than less innovative bird taxa when colonising new habitats. Moreover, innovative acts are most often performed during the cold season than outside winter in Western Palaearctic passerines, providing support for the idea that behavioural flexibility can help animals to cope with extreme variation in environmental conditions (Sol et al. 2005b). Finally, innovative, large-brained taxa seem to be more speciose than small-brained, non-innovative ones (Nicolakakis et al. 2003; Sol et al. 2005c), thereby bringing support to the idea that behavioural flexibility might be linked with high rates of evolution (Wyles 1983).

Despite the observation that behavioural flexibility can have a positive effect on survival, the ability to invent new solutions to recurrent or novel ecological problems seems to vary widely among taxa. For example, in birds, 30 genera account for more than half of the innovations (over a total of more than 2200 innovations; Lefebvre, unpubl. obs.), and some very-well studied genera show very few or no innovations at all. Only two innovations have been reported for Canada geese (*Branta canadensis*), for instance, despite the publication of 954 papers since 1978, and one innovation for pheasants despite 828 publications. In a hierarchical model of the control of learning strategies, Laland (2004) suggests that animals will resort to innovation only when unlearned strategies, individual learning of species-typical behavioural patterns, and social learning strategies have all proven ineffective at procuring resources. Indeed, animals are equipped with fine-tuned adaptations to the ecological problems they regularly meet, such that species-typical behaviours (unlearned or learned) most often provide a higher energetic return than alternative, innovative solutions (Laland 2004). When the rewards associated with commonly used behaviours decrease, social learning can provide an effective way to acquire novel behavioural patterns that are locally adaptive (Galef 1995), provided that there is a high frequency of demonstrators providing accurate information in the population (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985). Innovation might be rare because innovators must somehow block the expression of a common behaviour, which will only occur (1) when current solutions fail and/or (2) when the costs of trying new solutions are low (Hauser 2003).

The failure to obtain resources with usual behaviours can be associated with the hypothesis that "necessity is the mother of invention" (Reader & Laland 2003). From this hypothesis, we could expect hungry animals to show a higher propensity to innovate than animals that have already meet their energetic requirements. Psychologists discuss differences in motivation as a source of bias in how quickly animals can learn novel tasks, and it has been a standard practise for decades in experimental psychology to control as much as possible for differences in hunger levels between subjects (Bitterman 1965; Thorndike 1998). Individual differences in innovative propensity also provide support to the "necessity" hypothesis; in chimpanzees, dominant individuals have better access to resources, and have been found to innovate much less often than subordinates (Reader & Laland 2001). Laland & Reader (1999) showed that females, small individuals, as well as hungry individuals were more likely to innovate in guppies (*Poecilia reticulata*). The sex difference observed in this study was best interpreted in terms of sex differences in parental investment: because male guppies provide only sperm, their reproductive success is limited mainly by mating opportunities, while females' reproduction is mainly limited by access to resources (Davies 1991). This might also explain why male primates showed more courtship-related innovations than females (Reader & Laland 2001).

Individuals who can obtain a greater fitness return by engaging in innovative behaviours may thus be better inventors. However, these observations contrast with the high rates of innovations observed in provisioned populations and captive animals fed more or less *ab libitium*. In this case, it rather seems that it is the absence of necessity that creates a context where the costs of trying out new solutions in terms of time and energy invested are low, such as when young are under the care and protection of a parent (Kummer & Goodall 1985).

One important cost of innovation consists in investing time and energy in trying out new behavioural patterns that will not always lead to the acquisition of resources or that may lead to inefficient exploitation of the environment relative to species-typical options. Other costs of innovation include increased predation risk or various hazards in exploring novel parts of the environment (Reader & Laland 2003), and risks associated with the use of novel resources, such as the consumption of toxic or noxious items. For example, a pelican was found dead after consuming a stingray, an item not previously reported to be predated on by pelicans (Bostic & Banks 1966).

In addition to costs linked with the expression of innovative tendencies, there are also some costs associated with evolving the ability to innovate; the correlation of innovativeness with brain size (Lefebvre et al. 1997; Reader & Laland 2002) suggests that a large neural substrate might be required in order to explore efficiently novel parts of the environment, recognize and evaluate the palatability of novel resources, and/or invent new motor patterns necessary in the completion of tasks for which the species has not evolved specifically. The very high costs of developing and maintaining a large brain have often been discussed as a factor that might balance against the benefits of intelligence in the evolution of a large brain (Johnston 1982; Bennett & Harvey 1985a; Lefebvre et al. in press). Certain life-history traits might favour the evolution of large brains, and thus of intelligence. Longevity, and in particular a long period as an adult (Lefebvre et al. 2006), has been suggested to favour the evolution of learning abilities in general; novel solutions, be they species-typical or not, can then be exploited for a longer period (Ricklefs 2004).

One possible cost of intelligent behaviours: social exploitation

An additional cost to intelligent behaviour that has rarely been examined is social exploitation; the payoffs of using intelligent behaviours can be reduced dramatically if resources obtained using these behaviours are subject to exploitation by con- or heterospecifics. The exploitation of the food discoveries of other foragers, or scrounging (Giraldeau & Caraco 2000), can significantly decrease foraging returns to producers, the individuals responsible for the food discoveries (Barnard & Sibly 1981). Social foraging theory has underlined the "scrounging costs" of group foraging. In this thesis, I will examine the idea that there is a scrounging cost to the use of intelligent behaviours, focusing on a case of proto-tool use (Parker & Gibson 1977; Lefebvre et al. 2002).

In foraging, tools (external objects detached from their substrate and directly manipulated by the foot or beak; Beck 1980) and proto-tools (external objects not detached from the substrate; Parker & Gibson 1977) are often used in a context that allows social exploitation. There are several, non-mutually exclusive, reasons why scrounging (joining the discoveries of producing foragers; Giraldeau & Caraco 2000) and kleptoparasitism (food-stealing; Brockmann & Barnard 1979) can be expected on tool and proto-tool behaviours. First, some tool-use behaviours are performed at increased rates in contexts of food scarcity (Tebbich et al. 2002; Moura & Lee 2004). During food shortage, the acquisition of food resources may make the difference between survival and death of individuals, and the relative value of food items is then extremely high. These conditions contribute to increased relative payoffs to kleptoparasitism compared with a strategy of searching for scarce items (Brockmann & Barnard 1979). Second, tool-related behaviours are usually performed to obtain large items with a high nutritive content (e.g. crows take mainly large whelks for aerial dropping; Zach 1978). Large and nutritious items have often been shown to be preferential targets of kleptoparasites (Brockmann & Barnard 1979). Third, tool-use may imply a large time investment in searching for a suitable tool, modifying it, and using it (e.g. chimpanzees must find a suitable twig, prepare it by stripping off leaves, insert the twig in the termite mound, and wait for ants to climb onto it; van Lawick-Goodall 1970). This investment increases the relative value of items obtained using tools and would favour the use of kleptoparasitism over honest foraging strategies to obtain these items. Fourth, many tool-related behaviours involve releasing the item during handling (e.g. dropping items on the ground, on an anvil, or in water; hammering items with a hard tool; wedging or impaling items to maintain their position; Beck 1980) and might thus include vulnerable handling time due to the reduced ability of animals to defend items that are not held in the bill, hand or feet. Also, tools might be located in a predictable area, where there might be an accumulation of conspecifics, leading to a higher probability of kleptoparasitism on these items (Brockmann & Barnard 1979). Finally, tool-related techniques require considerable motor skills (Iwaniuk et al. in prep.) and might be difficult to learn (e.g. juveniles are often less efficient than adults; Ingolfsson & Estrella 1978; Ottoni et al. 2005). The need to invest considerable time and energy in developing tool-using skills also contributes to increasing the relative payoffs of using kleptoparasitic tactics compared with learning and executing the behaviour.

The reduction in payoffs to intelligent behaviours due to social exploitation can lead to a decrease in the expression of these behaviours and their learning (e.g. an innovative solution leading to no reward to the innovator will probably not be repeated and might be lost). Some researchers have noted that individuals would sometimes refrain from expressing a learned technique in the presence of potential kleptoparasites (Visalberghi & Fragaszy 1990; Tokida et al. 1994). If this is of common occurrence, rates of expression of intelligent behaviour might not reflect the frequency of individuals in a population that have learned a technique or are able to perform a specific behaviour (Drea & Wallen 1999), because there might be some inhibition of expression of the behaviour under the risk of kleptoparasitism. Moreover, the use of intraspecific kleptoparasitism by part of the population reduces the proportion of individuals producing resources and might create a situation where payoffs obtained by individuals depend on the frequency of individuals engaged in both tactics (Barnard & Sibly 1981).

Costs and benefits of a foraging innovation

Famous examples of animal innovation include the opening of milk bottles by British tits (Fisher & Hinde 1949) and the washing of wheat and sweet potatoes by Japanese macaques (Kawai 1965). These observations have led to the development of a sub-field of animal behaviour dedicated to the study of innovations and their transmission in populations. Researchers in this field ask questions such as: Who are the innovators? How is the innovation transmitted from one individual to another? What factors prevent or favour cultural transmission? (reviewed in the book edited by Reader & Laland 2003). In this literature, however, the costs and benefits of innovative behaviours are rarely tackled (Lee 2003). In my thesis, I adopt a behavioural ecology approach and conduct the first investigation of costs and benefits of a foraging innovation by wild birds: dunking behaviour in Carib grackles (*Quiscalus lugubris*) of Barbados. Dunking behaviour consists in the immersion of food items in water. It had not been reported in *Q. lugubris* before Louis Lefebvre and Simon Reader witnessed grackles repeatedly dropping and retrieving bread pieces in a rain puddle in 2001 (see fig 1.). Following the definition of Lefebvre and colleagues (1997), food-dunking in Carib grackles qualifies as a foraging innovation, as the behaviour had not been reported before for this species. It is highly unlikely that the dunking behaviour observed represented random dropping of the food because the puddle covered less than 2 % of the terrace area (Morand-Ferron et al. 2004). Moreover, the behaviour was observed to occur again at this site, and at three other sites nearby, so that we could rule out the possibility that the initial observation was a one-time chance occurrence. Inquiries to local ornithologists revealed that dunking has indeed been witnessed before in Barbados, but that it is highly unusual behaviour (Frost, pers. comm.).

Dunking seems to be a heterogeneous behavioural category in terms of function. Indeed, diverse behaviours such as a hawk drowning a magpie by holding it under water (Drew 1997), monkeys washing items by shaking them and rubbing them under water (Kawai 1965) and a blackbird transporting water to its nestlings by immersing crickets into water before bringing then to the nest (Koenig 1985) can all be joined under the term "dunking". Depending on the putative function of the behaviour, dunking can be classified as a case of proto- or true tool use. As a food-processing behaviour allowing softening, washing, or drowning prey, dunking is a proto-tool behaviour as it involves the use of an un-detached element of the environment that is not directly held by the animal (Parker & Gibson 1977). However, when food is used as a container or a sponge to transport water to a remote site, then the behaviour can be considered as a true tool-use case (Beck 1980).

Observers of dunking behaviour are often struck by its apparent ingenuity (Seibt & Wickler 1978; Gerig 1979) and some have even suggested that the low rate of dunking in the field might point to insight learning or some other complex cognitive processes (Pitochelli 1985). In this thesis, I do not attempt to understand these putative cognitive processes, which an experimental approach like that used by Clayton and colleagues on episodic memory would be most appropriate to study. Instead, I assume that a behaviour that satisfies the criteria of innovativeness and proto-tool use in an opportunistic generalist passeriform is a good model to study social exploitation as a cost of animal intelligence. Innovativeness and tool use are included in several recent operational definitions of animal intelligence (Reader & Laland 2002; Seyfarth & Cheney 2002; Marino 2005; Sherry 2006).

In Chapter 1 of this thesis, I address the question of rarity of dunking behaviour: is dunking rare because it has been invented by only a few individuals and has not spread to the whole population, or is it rare because the net benefits obtained by dunking food are lower than not dunking in most field conditions? Field observations documenting rates of dunking in wild grackles first revealed that the frequency of dunking in the field is not fixed, but is influenced by food characteristics and social context. Moreover, almost all captive birds held in isolation and observed under conditions favourable to the expression of dunking did perform the behaviour. This suggests that Carib grackles might have a predisposition to learn this specific behaviour, in a similar manner that New Caledonian crows and woodpecker finches have a predisposition for twigs or leaves tool-use, or that Carib grackles are proficient learners in general (*Quiscalus* is the most innovative genus of North American passerines after *Corvus*; Lefebvre, unpubl. data). This investigation of costs and benefits to the behaviour allowed us to provide conditions in the field that increased the frequency of observation of dunking behaviour from practically nil in normal conditions around Barbados to as much as 70 % in controlled field conditions.

In Chapter 1, I show that grackles dunk dry and hard food items more often than fresh and soft items. Chapter 2 provides a further test of the hypothetical function of dunking as a food-processing technique easing the ingestion of items that are difficult to swallow. I show that hard items can be ingested more quickly when dunked in water than when eaten dry, suggesting that dunking is a proto-tool food-processing technique. As Chapter 1 pointed to kleptoparasitism by conspecifics as the main cost related to dunking items in water, Chapter 2 explores in more details which differences in the behaviour of dunking versus non-dunking birds lead to an increased probability of food theft in the former. This allows an examination of the hypotheses discussed above, namely that tool-related behaviours increase vulnerability to kleptoparasitism because they involve (1) profitable items, (2) the use of an element of the environment where the density of potential kleptoparasites is high and (2) a momentarily loss of physical control over food items.

In Chapter 3, I examine food-processing through dunking behaviour and kleptoparasitism of processed items by Carib grackles as two alternative foraging tactics, and make predictions on the frequency of use of these tactics in different conditions within a producer-scrounger game-theoretical framework. This chapter addresses the frequency-dependence element of this system; it shows that kleptoparasites do best when they are few in the group, and investigates how changes observed at the group level are brought about at the level of individual behaviour. Chapter 4 takes a more general approach to the phenomenon of avian kleptoparasitism and tests both classic and novel hypotheses on the factors that have favoured the evolution of food-stealing in birds.

Approaches used in this thesis

Overall, the thesis uses four methods: observations in the field, experiments in captivity and in the field, game theory models and comparative methods on taxonomic distributions, to address its main question: what is the relationship between cognition and its exploitation by food theft? It does this on all birds (chapter 4) and in one test case on one species, Carib grackle dunking behaviour (chapter 1, 2 and 3).

Contributions to knowledge

Chapter 1 is the first study on avian dunking behaviour, and includes a complete list of all cases reported up to 2004. Dunking behaviour has been studied mostly in primates (e.g. Visalberghi & Fragaszy 1990), due to the strong interest in learning processes leading to the adoption of potato-washing and wheat placer-mining behaviours in the provisioned troop of Japanese macaques on Koshima islet (Kawai 1965). In general, innovative behaviours have mostly been studied through the comparative method, in which researchers test the association between the frequency of innovative behaviours and the size of neurological substrate or other measures of cognitive abilities (reviewed in Lefebvre et al. 2004). Studies on specific innovative behaviours most often constitute in the examination of learning processes (e.g. Palameta & Lefebvre 1985, Fragaszy & Visalberghi 1990) or of individual differences (e.g. Laland & Reader 1999, Pfeffer et al. 2002) on a laboratory-based task. Here, I adopt a behavioural ecology approach and present one of the first examinations of costs and benefits of an innovative behaviour in the field. An important contribution of the chapter is the proposal that behaviours performed at a low rate in a population should not be taken as evidence that the behaviour can be learned only by a part of the population and/or relies on complex cognitive processes, but instead that researchers should investigate costs and benefits to the behaviour and test the ability of individuals to perform or learn to execute the behaviour in a context where the net benefits to the behaviour are higher than alternative foraging tactics.

Chapter 2 explores determinants of kleptoparasitic acts in Carib grackles, but provides a more general view than most field studies on kleptoparasitic host selection by taking into account the behaviour of both kleptoparasites and hosts. It addresses the original question as to whether and how tool-related behaviours render animals more vulnerable to exploitation. It also reveals two anti-kleptoparasitic tactics used by grackles to reduce their losses to conspecifics, providing further support for the view that dunking behaviour is not executed as a fixed, stereotyped behavioural pattern, but varies in frequency (Chapter 1) and form of expression (Chapter 2) according to local variation in costs and benefits to the behaviour. The use of anti-kleptoparasitic behaviours by animals engaged in an innovative proto-tool behaviour suggests that the avoidance of exploitation might not only lead to a reduction in the rate of expression of intelligent behaviours, but might also select for the ability to invent counter-tactics reducing losses to kleptoparasites.

Chapter 3 builds on the findings on the previous two chapters revealing dunking behaviour as a flexible food-processing technique. It looks at dunking and its exploitation using a producer-scrounger game-theoretical framework, and provides the first evidence for the basic assumption of negative frequency-dependence of scroungers' payoffs in a wild animal. Examining dunking and kleptoparasitism within this framework allowed making predictions on the use of these two alternative tactics by groups of Carib grackles under changes in local foraging conditions, allowing a fuller understanding of foraging decisions by wild Carib grackles. Chapter 3 constitutes the first study in which the costs of both producing and scrounging were manipulated by the experimenter in the field, and in which adjustments in tactic use following changes in local foraging condition are documented both at the group and individual level. It also allowed new insights on the effect of change in scrounger frequency on group size as the birds were free to join or leave the experimental food patch, which is usually not possible in captive experiments.

Chapter 4 provides the first comprehensive review of avian kleptoparasitic cases in the literature since Brockmann and Barnard's 1979 review. This work constitutes the first comparative test on the ecological, behavioural and morphological characteristics of avian kleptoparasites worldwide. In addition to providing a rigorous test of classic predictions on the evolution of food-stealing in birds, it brings along a novel conception of kleptoparasitism as a tactical behaviour performed by large-brained birds. This chapter uses a novel statistical method for taking into account phylogenetic relationships between taxa ("phylogenetic GEE") and provides suggestions for future studies about the importance of cognition in exploitative relationships.

Appendix I extends the investigation of the function of dunking behaviour to another avian system, *Corvus brachyrhynchos*, which is part of the family of birds with the largest number of reports on dunking behaviour (seven species out of 42 in Corvidae). This short communication constitutes the first report of dunking in wild American crows, thereby exemplifying the type of publication contributing to the building of the innovation database.

References

Alatalo, R. V., Gustafsson, L., Linden, M. & Lundberg, A. 1985. Interspecific competition and niche shifts in tits and the goldcrest - An experiment. Journal of Animal Ecology, 54, 977-984.

Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers - A general model and its application to captive flocks of house sparrows. Animal Behaviour, 29, 543-550.

Barton, R. A. 1996. Neocortex size and behavioural ecology in primates. Proceedings of the Royal Society of London Series B-Biological Sciences, 263, 173-177.

Beck, B. B. 1980. Animal tool behavior: the use and manufacture of tools by animals. New York: Garland.

Bennett, P. M. & Harvey, P. H. 1985a. Brain size, development and metabolism in birds and mammals. Journal of Zoology, 207, 491-509.

Bennett, P. M. & Harvey, P. H. 1985b. Relative brain size and ecology in birds. Journal of Zoology, 207, 151-169.

Berger, J., Swenson, J. E. & Persson, I. L. 2001. Recolonizing carnivores and naive prey: Conservation lessons from Pleistocene extinctions. Science, 291, 1036-1039.

Bermejo, M. & Illera, G. 1999. Tool-set for termite-fishing and honey extraction by wild chimpanzees in the Lossi Forest, Congo. Primates, 40, 619-627.

Bitterman, M. E. 1965. Phyletic differences in learning. American Psychologist, 20, 396-410.

Boag, P. T. & Grant, P. R. 1981. Intense natural selection in a population of Darwin Finches (Geospizinae) in the Galapagos. Science, 214, 82-85.

Boesch, C. 1996. Animal behaviour - The question of culture. Nature, 379, 207-208.

Bond, A. B., Kamil, A. C. & Balda, R. P. 2003. Social complexity and transitive inference in corvids. Animal Behaviour, 65, 479-487.

Bostic, D. L. & Banks, R. C. 1966. A record of stingray predation by brown pelican. Condor, 68, 515-&.

Boyd, R. & Richerson, P. J. 1985. Culture and the evolutionary process. Chicago: University of Chicago Press.

Brockmann, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. Animal Behaviour, 27, 487-514.

Brooke, M. D., Davies, N. B. & Noble, D. G. 1998. Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. Proceedings of the Royal Society of London Series B-Biological Sciences, 265, 1277-1282.

Bugnyar, T. & Heinrich, B. 2005. Ravens, *Corvus Corax*, differentiate between knowledgeable and ignorant competitors. Proceedings of the Royal Society B-Biological Sciences, 272, 1641-1646.

Burish, M. J., Kueh, H. Y. & Wang, S. S. H. 2004. Brain architecture and social complexity in modern and ancient birds. Brain Behavior and Evolution, 63, 107-124.

Byrne, R. W. & Whiten, A. 1988. Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes and humans. Oxford: Clarendon Press.

Call, J. 2001. Chimpanzee social cognition. Trends in Cognitive Sciences, 5, 388-393.

Cavalli-Sforza, L.L. & Feldman, M. W. 1981. Cultural transmission and evolution: a quantitative approach. Princeton: Princeton University Press.

Chappell, J. & Kacelnik, A. 2002. Tool selectivity in a non-Primate, the New Caledonian crow (*Corvus Moneduloides*). Animal Cognition, 5, 71-78.

Chomsky, N. 1972. Language and mind. New York: Harcourt Brace Jovanovich.

Clayton, N. S. & Dickinson, A. 1998. Episodic-like memory during cache recovery by scrub jays. Nature, 395, 272-274.

Cluttonbrock, T. H. & Harvey, P. H. 1980. Primates, brains and ecology. Journal of Zoology, 190, 309-323.

Darwin, C. 1871. The descent of man and selection in relation to sex. London: Murray.

Davidar, E. R. D. 1991. Common myna *Acridotheres tristis* fishing. Journal of the Bombay Natural History Society, 88, 287.

Davies, N. B. 1991. Mating systems. In: Behavioural ecology: an evolutionary approach. 3rd ed. (Ed. by J. R. Krebs & N. B. Davies), pp. 263-294. Oxford: Blackwell Publishing.

De Kort, S. R., Dickinson, A. & Clayton, N. S. 2005. Retrospective cognition by food-caching Western scrub-jays. Learning and Motivation, 36, 159-176.

de Waal, F. B. M., Dindo, M., Freeman, C. A. & Hall, M. J. 2005. The monkey in the mirror: hardly a stranger. Proceedings of the National Academy of Sciences of the United States of America, 102, 11140-11147.

de Winter, W. & Oxnard, C. E. 2001. Evolutionary radiations and convergences in the structural organization of mammalian brains. Nature, 409, 710-714.

Devoogd, T. J., Krebs, J. R., Healy, S. D. & Purvis, A. 1993. Relations between song repertoire size and the volume of brain nuclei related to song - Comparative evolutionary analyses amongst Oscine birds. Proceedings of the Royal Society of London Series B-Biological Sciences, 254, 75-82.

Drea, C. M. & Wallen, K. 1999. Low-status monkeys "play dumb" when learning in mixed social groups. Proceedings of the National Academy of Sciences of the United States of America, 96, 12965-12969.

Drew, C. C. 1997. Eurasian sparrowhawk drowning magpie. British Birds, 90, 524-525.

Emery, N. J. 2006. Cognitive ornithology: the evolution of avian intelligence. Philosophical Transactions of the Royal Society B-Biological Sciences, 361, 23-43.

Emery, N. J. & Clayton, N. S. 2001. Effects of experience and social context on prospective caching strategies by scrub jays. Nature, 414, 443-446.

Emery, N. J. & Clayton, N. S. 2004a. Comparing the complex cognition of birds and primates. In: Comparative vertebrate cognition, (Ed. by L. J. Rogers and G. Kaplan), pp. 3-53, New York: Kluwer Academic.

Emery, N. J. & Clayton, N. S. 2004b. The mentality of crows: convergent evolution of intelligence in corvids and apes. Science, 306, 1903-1907.

Estes, J. A., Tinker, M. T., Williams, T. M. & Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. Science, 282, 473-476.

Finlay, B. L. & Darlington, R. B. 1995. Linked regularities in the development and evolution of mammalian brains. Science, 268, 1578-1584.

Fischer, J. & Hinde, R. A. 1949. The opening of milk bottles by birds. British Birds, 42, 347-357.

Fox, L. R. & Morrow, P. A. 1981. Specialization - Species property or local phenomenon. Science, 211, 887-893.

Fragaszy, D. M. & Visalberghi, E. 1990. Social processes affecting the appearance of innovative behaviors in capuchin monkeys. Folia Primatologica, 54, 155-165.

Galef, B. G. 1995. Why behavior patterns that animals learn socially are locally adaptive. Animal Behaviour, 49, 1325-1334.

Gallup, G. G. 1970. Chimpanzees self-recognition. Science, 167, 86-&.

Garamszegi, L. Z. & Eens, M. 2004. The evolution of hippocampus volume and brain size in relation to food hoarding in birds. Ecology Letters, 7, 1216-1224.

Gardner, R. A. & Gardner, B. T. 1969. Teaching sign language to a chimpanzee. Science, 165, 664-669.

Gerig, R. 1979. Death by drowning – One Cooper's hawk approach. American Birds 33, 836.

Giraldeau, L.-A. & Caraco, T. 2000. Social foraging theory. Princeton: Princeton University Press.

Gittleman, J. L. 1994. Female brain size and parental care in Carnivores. Proceedings of the National Academy of Sciences of the United States of America, 91, 5495-5497.

Goodwin, D. 1986. Crows of the world, 2nd ed. British Museum: England.

Gossette, R. L. 1968. Examination of retention decrement explanation of comparative successive discrimination reversal learning by birds and mammals. Perceptual and Motor Skills, 27, 1147-&.

Gould, J. L. 2004. Animal cognition. Current Biology, 14, R372-R375.

Halsey, L. G., Bezerra, B. M. & Souto, A. S. 2006. Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? Animal Cognition, 9, 229-233.

Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E. 2003. Do capuchin monkeys, *Cebus apella*, know what conspecifics do and do not see? Animal Behaviour, 65, 131-142.

Hare, B., Call, J. & Tomasello, M. 2001. Do chimpanzees know what conspecifics know? Animal Behaviour, 61, 139-151.

Harvey, P. H., Cluttonbrock, T. H. & Mace, G. M. 1980. Brain size and ecology in small mammals and primates. Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences, 77, 4387-4389.

Hauser, M D. 2003. To innovate or not to innovate? That is the question. In: Animal innovation, (Ed. by S. M. Reader & K. N. Laland), pp. 329-338. Oxford: Oxford University Press.

Hauser, M. D., Chomsky, N. & Fitch, W. T. 2002. The faculty of language: what is it, who has it, and how did it evolve? Science, 298, 1569-1579.

Healy, S. D., De Kort, S. R. & Clayton, N. S. 2005. The hippocampus, spatial memory and food hoarding: a puzzle revisited. Trends in Ecology & Evolution, 20, 17-22.

Heinrich, B. 1995. An experimental investigation of insight in Common Ravens (*Corvus corax*). Auk, 112, 994-1003.

Herman, L. M., Richards, D. G. & Wolz, J. P. 1984. Comprehension of sentences by bottlenosed dolphins. Cognition, 16, 129-219.

Hodos, W. & Campbell, C. B. 1969. Scala Naturae - Why there is no theory in comparative psychology. Psychological Review, 76, 337-&.

Humphrey, N. K. 1976. The social function of intellect. In: Growing points in ethology, (Ed. by P. P. G. Bateson & R. A. Hinde), pp. 303-317. Cambridge: Cambridge University Press.

Ingolfsson, A. & Estrella, B. T. 1978. Development of shell-cracking behavior in herring gulls. Auk, 95, 577-579.

Jackson, J. 1985. The dunking habit of common grackles. American Birds 39, 261-262.

Jerison, H. J. 1973. Evolution of the brain and intelligence. New York: Academic Press.

Johnston, T. D. 1982. Selective costs and benefits in the evolution of learning. Advances in the Study of Behavior, 12, 65-106.

Jolly, A. 1966. Lemur social behavior and primate intelligence - Step from prosimian to monkey intelligence probably took place in a social context. Science, 153, 501-504.

Kamil, A. C. 1988. A synthetic approach to the study of animal intelligence. In: Comparative perspectives in modern psychology. (ED. by W.D. Leger), pp. 230-257. Lincoln: University of Nebraska Press.

Kamiski, J., Call, J. & Fischer, J. 2004. Word learning in a domestic dog: evidence for "fast mapping". Science, 304, 1682-1683.

Kawai, M. 1965. Newly-acquired pre-cultural behaviour of the natural troop of Japanese monkeys on Koshima islet. Primates, 6, 1-30.

Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A. 2005. Tool manufacture by naive juvenile crows. Nature, 433, 121-121.

Kerr, B. & Feldman, M. W. 2003. Carving the cognitive niche: optimal learning strategies in homogeneous and heterogeneous environments. Journal of Theoretical Biology, 220, 169-188.

Klopfer, P. H. 1967. Behavioral stereotypy in birds. Wilson Bulletin, 79, 290-&.

Koenig, W. D. 1985. Dunking of prey by Brewer's blackbirds: a novel source of water for nestlings. Condor, 87, 444-445.

Köhler, W. 1927. The mentality of apes. New York: Vontage Books.

Krebs, J. R., Healy, S. D. & Shettleworth, S. J. 1990. Spatial memory of Paridae - Comparison of a storing and a nonstoring species, the coal tit, *Parus ater*, and the great tit, *P. Major*. Animal Behaviour, 39, 1127-1137.

Krebs, J. R., Sherry, D. F., Healy, S. D., Perry, V. H. & Vaccarino, A. L. 1989. Hippocampal specialization of food-storing birds. Proceedings of the National Academy of Sciences of the United States of America, 86, 1388-1392.

Kudo, H. & Dunbar, R. I. M. 2001. Neocortex size and social network size in primates. Animal Behaviour, 62, 711-722.

Kummer, H. & Goodall, J. 1985. Conditions of innovative behavior in primates. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 308, 203-214.

Laland, K. N. 2004. Social learning strategies. Learning & Behavior, 32, 4-14.

Laland, K. N. & Reader, S. M. 1999. Foraging innovation in the guppy. Animal Behaviour, 57, 331-340.

Lee, P. C. 2003. Innovation as a behavioural response to environmental challenges: a cost and benefit approach. In: Animal innovation, (Ed. by S. M. Reader & K. N. Laland), pp. 261-277. Oxford: Oxford University Press.

Lefebvre, L. & Bolhuis, J. J. 2003. Positive and negative correlates of feeding innovations in birds: evidence for limited modularity. In: Animal innovation, (Ed. by S. M. Reader & K. N. Laland), pp. 39-61. Oxford: Oxford University Press.

Lefebvre, L., Gaxiola, A., Dawson, S., Timmermans, S., Rosza, L. & Kabai, P. 1998. Feeding innovations and forebrain size in Australasian birds. Behaviour, 135, 1077-1097.

Lefebvre, L. & Giraldeau, L.-A. 1996. Is social learning an adaptive specialization? In: Social learning in animals: the roots of culture, (Ed. by C. M. Heyes and B. G. Galef, Jr), pp. 107-128. San Diego: Academic Press.

Lefebvre, L., Marino, L, Sol, D., Lemieux-Lefebvre, S. & Arshad, S. 2006. Large brains and lengthened life history periods in Odontocetes. Brain Behavior and Evolution, 68, 218-228.

Lefebvre, L., Nicolakakis, N. & Boire, D. 2002. Tools and brains in birds. Behaviour, 139, 939-973.

Lefebvre, L., Reader, S. M., & Boire, D. 2007. The evolution of encephalization. In: The evolution of nervous systems, ed. J. Kaas, In Press.

Lefebvre, L., Reader, S. M. & Sol, D. 2004. Brains, innovations and evolution in birds and primates. Brain Behavior and Evolution, 63, 233-246.

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997. Feeding innovations and forebrain size in birds. Animal Behaviour, 53, 549-560.

Lucas, J. R., Brodin, A., De Kort, S. R. & Clayton, N. S. 2004. Does hippocampal size correlate with the degree of caching specialization? Proceedings of the Royal Society of London Series B-Biological Sciences, 271, 2423-2429.

Macphail, E. M. 1985. Vertebrate intelligence - The null hypothesis. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences, 308, 37-51.

Macphail, E. M. 1987. The comparative psychology of intelligence. Behavioral and Brain Sciences, 10, 645-656.

Macphail, E. M. & Bolhuis, J. J. 2001. The evolution of intelligence: adaptive specializations versus general process. Biological Reviews, 76, 341-364.

Madden, J. 2001. Sex, bowers and brains. Proceedings of the Royal Society of London Series B-Biological Sciences, 268, 833-838.

Marino, L. 2005. Big brains do matter in new environments. Proceedings of the National Academy of Sciences of the United States of America, 102, 5306-5307.

Morand-Ferron, J., Lefebvre, L., Reader, S. M., Sol, D. & Elvin, S. 2004. Dunking behaviour in Carib grackles. Animal Behaviour, 68, 1267-1274.

Moura, A. C. D. & Lee, P. C. 2004. Capuchin stone tool use in Caatinga dry forest. Science, 306, 1909-1909.

Mulcahy, N. J. & Call, J. 2006. How great apes perform on a modified trap-tube task. Animal Cognition, 9, 193-199.

Nicolakakis, N. & Lefebvre, L. 2000. Forebrain size and innovation rate in European birds: feeding, nesting and confounding variables. Behaviour, 137, 1415-1429.

Nicolakakis, N., Sol, D. & Lefebvre, L. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. Animal Behaviour, 65, 445-452.

Nottebohm, F. 1981. A brain for all seasons - Cyclical anatomical changes in song control. Science, 214, 1368-1370.

Oakley, K. P. 1959. Man the tool-maker. 2nd ed. Chicago: University of Chicago Press.

Osthaus, B., Lea, S. E. G. & Slater, A. M. 2005. Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. Animal Cognition, 8, 37-47.

Ottoni, E. B., De Resende, B. D. & Izar, P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus Apella*) know about others' tool-using skills. Animal Cognition, 8, 215-219.

Owens, I. P. F., Bennett, P. M. & Harvey, P. H. 1999. Species richness among birds: body size, life history, sexual selection or ecology? Proceedings of the Royal Society of London Series B-Biological Sciences, 266, 933-939.

Palameta, B. & Lefebvre, L. 1985. The social transmission of a food-finding technique in pigeons: what is learned? Animal Behaviour, 33, 892-896.

Parker, S. T. & Gibson, K. R. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. Journal of Human Evolution, 6, 623-641.

Paz-y-Mino, G., Bond, A. B., Kamil, A. C. & Balda, R. P. 2004. Pinyon jays use transitive inference to predict social dominance. Nature, 430, 778-781.

Pearce, J. M. 1997. Animal learning and cognition - An introduction. Hove, Sussex: Psychology Press.

Pepperberg, I. M. 2002. In search of King Solomon's ring: cognitive and communicative studies of grey parrots (*Psittacus erithacus*). Brain Behavior and Evolution, 59, 54-67.

Pfeffer, K, Fritz, J. & Kortschal, K. 2002. Hormonal correlates of being an innovative Greylag goose. Animal Behaviour 63, 687-695.

Phillimore, A. B., Freckleton, R. P., Orme, C. D. L. & Owens, I. P. F. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. American Naturalist, 168, 220-229.

Pitochelli, J. 1985. Apparent insight learning by some common grackles breeding in Central Park, New York. Kingbird, Winter, 32-33.

Povinelli, D. J. 2000. Folk physics for apes. New York: Oxford University Press.

Povinelli, D. J., Gallup, G. G., Eddy, T. J., Bierschwale, D. T., Engstrom, M. C., Perilloux, H. K. & Toxopeus, I. B. 1997. Chimpanzees recognize themselves in mirrors. Animal Behaviour, 53, 1083-1088.

Premack, D. 1971. Language in chimpanzee. Science, 172, 808-&.

Premack, D. & Woodruff, G. 1978. Does the chimpanzee have a theory of mind. Behavioral and Brain Sciences, 1, 515-526.

Rand, A. L. 1967. A common grackle learning to soak bread. Wilson Bulletin 79, 455-456.

Ratcliffe, J. M., Fenton, M. B. & Shettleworth, S. J. 2006. Behavioral flexibility positively correlated with relative brain volume in predatory bats. Brain Behavior and Evolution, 67, 165-176.

Reader, S. M. & Laland, K. N. 2001. Primate innovation: sex, age and social rank differences. International Journal of Primatology, 22, 787-805.

Reader, S. M. & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences of the United States of America, 99, 4436-4441.

Reader, S. M. & Laland, K. N., Eds. 2003. Animal innovation. Oxford: Oxford University Press.

Reader, S. M. & Laland, K. N. 2003. Animal innovation: an introduction. In: Animal innovation, (Ed. by S. M. Reader & K. N. Laland), pp. 3-35. Oxford: Oxford University Press.

Reboreda, J. C., Clayton, N. S. & Kacelnik, A. 1996. Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. Neuroreport, 7, 505-508.

Reiner, A., Yamamoto, K. & Karten, H. J. 2005. Organization and evolution of the avian forebrain. Anatomical Record Part a-Discoveries in Molecular Cellular and Evolutionary Biology, 287A, 1080-1102.

Reiss, D. & Marino, L. 2001. Mirror self-recognition in the bottlenose dolphin: a case of cognitive convergence. Proceedings of the National Academy of Sciences of the United States of America, 98, 5937-5942.

Ricklefs, R. E. 2004. The cognitive face of avian life histories - The 2003 Margaret Morse Nice Lecture. Wilson Bulletin, 116, 119-133.

Riddell, W. I. & Corl, K. G. 1977. Comparative investigation of relationship between cerebral indexes and learning abilities. Brain Behavior and Evolution, 14, 385-398.

Rogers, E. M. 1993. Diffusion of innovations. New York: Free Press.

Romanes, G. J. 1883. Animal intelligence. New York: D. Appleton and cie.

Sakura, O. & Matsuzawa, T. 1991. Flexibility of wild chimpanzee nut-cracking behavior using stone hammers and anvils - an experimental analysis. Ethology, 87, 237-248.

Scott, S. N., Clegg, S. M., Blomberg, S. P., Kikkawa, J. & Owens, I. P. F. 2003. Morphological shifts in island-dwelling birds: the roles of generalist foraging and niche expansion. Evolution, 57, 2147-2156.

Seibt, U. & Wickler, W. 1978. Marabou storks wash dung beetles. Zeitschrift fur Tierpsychologie, 46, 324-327.

Seyfarth, R. M. & Cheney, D. L. 2000. Social awareness in monkeys. American Zoologist, 40, 902-909.

Seyfarth, R. M. & Cheney, D. L. 2002. What are big brains for? Proceedings of the National Academy of Sciences of the United States of America, 99, 4141-4142.

Seyfarth, R. M & Cheney, D. L. 2003. The structure of social knowledge in monkeys. In: Animal social complexity, (Ed. by F. B. M. de Waal & P. L. Tyack), pp. 207-229. Cambridge: Harvard University Press.

Sherry, D. F. 2006. Neuroecology. Annual Review of Psychology, 57, 167-197.

Sherry, D. F., Forbes, M. R. L., Khurgel, M. & Ivy, G. O. 1993. Females have a larger hippocampus than males in the brood-parasitic brown-headed cowbird. Proceedings of the National Academy of Sciences of the United States of America, 90, 7839-7843.

Sherry, D. F. & Schacter, D. L. 1987. The evolution of multiple memory systems. Psychological Review, 94, 439-454.

Sherry, T. W. 1990. When are birds dietarily specialized? Distinguishing ecological from evolutionary approaches. Studies in Avian Biology, 13, 337-352.

Shettleworth, S. J. 1998. Cognition, evolution, and behaviour. Oxford: Oxford University Press.

Sol, D. 2003. Behavioural innovations: a neglected issue in the ecological and evolutionary literature? In: Animal innovation, (Ed. by S. M. Reader & K. N. Laland), pp. 65-82. Oxford: Oxford University Press.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005a. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America, 102, 5460-5465.

Sol, D., Lefebvre, L. & Rodriguez-Teijeiro, J. D. 2005b. Brain size, innovative propensity and migratory behaviour in temperate Palaearctic birds. Proceedings of the Royal Society B-Biological Sciences, 272, 1433-1441.

Sol, D., Stirling, D. G. & Lefebvre, L. 2005c. Behavioral drive or behavioral inhibition in evolution: subspecific diversification in holarctic passerines. Evolution, 59, 2669-2677.

Suddendorf, T. & Busby, J. 2003. Mental time travel in animals? Trends in Cognitive Sciences, 7, 391-396.

Stephens, D. W. 1991. Change, regularity, and value in the evolution of learning. Behavioral Ecology, 2, 77-89.

Szekely, T., Catchpole, C. K., DeVoogd, A., Marchl, Z. & DeVoogd, T. J. 1996. Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae). Proceedings of the Royal Society of London Series B-Biological Sciences, 263, 607-610.

Tebbich, S. & Bshary, R. 2004. Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. Animal Behaviour, 67, 689-697.

Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. 2001. Do woodpecker finches acquire tool-use by social learning? Proceedings of the Royal Society of London Series B-Biological Sciences, 268, 2189-2193.

Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M. 2002. The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). Ecology Letters, 5, 656-664.

Terkel, J. 1995. Cultural transmission in the black rat - Pine-cone feeding. In: Advances in the Study of Behavior, 24, 119-154.

Thorndike, E. L. 1998. Animal intelligence - An experimental study of the associate processes in animals. American Psychologist, 53, 1125-1127.

Thorpe, W. H. 1963. Learning and instinct in animals. London: Methuen & Co. Ltd.

Timmermans, S., Lefebvre, L., Boire, D. & Basu, P. 2000. Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. Brain Behavior and Evolution, 56, 196-203.

Tokida, E., Tanaka, I., Takefushi, H. & Hagiwara, T. 1994. Tool-using in Japanese Macaques - Use of stones to obtain fruit from a pipe. Animal Behaviour, 47, 1023-1030.

Tulving, E. 1983. Elements of episodic memory. Oxford: Clarendon Press.

van Lawick-Goodall, J. 1970. Tool-using primates and other vertebrates. Advances in the Study of Behaviour, 3, 195-249.

van Schaik, C. P., Noordwijk, M. A. & Wich, S. A. 2006. Innovation in wild Bornean orangutans. Behaviour, 143, 839-876.

Vickery, W. L., Giraldeau, L. A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991. Producers, scroungers, and group foraging. American Naturalist, 137, 847-863.

Visalberghi, E. & Fragaszy, D. M. 1990. Food-washing behavior in tufted capuchin monkeys, *Cebus apella*, and crabeating macaques, *Macaca fascicularis*. Animal Behaviour, 40, 829-836.

Visalberghi, E. & Limongelli, L. 1994. Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology, 108, 15-22.

Werdenich, D. & Huber, L. 2006. A case of quick problem solving in birds: string pulling in keas, *Nestor notabilis*. Animal Behaviour, 71, 855-863.

Werner, T. K. & Sherry, T. W. 1987. Behavioral feeding specialization in *Pinaroloxias Inornata*, the Darwin finch of Cocos Island, Costa Rica. Proceedings of the National Academy of Sciences of the United States of America, 84, 5506-5510.

Wyles, J. S., Kunkel, J. G. & Wilson, A. C. 1983. Birds, behavior, and anatomical evolution. Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences, 80, 4394-4397.

Wynn, T. 1988. Tools and the evolution of human intelligence. In: Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans, (Ed. by R. W. Byrne and A. Whiten), pp. 272-284. Oxford: Clarendon Press.

Zach, R. 1978. Selection and dropping of whelks by Northwestern crows. 134-148.

Fig. 1. Carib grackles dunking bread in a rain puddle on the Seabourne terrace of the Bellairs Research Institute of McGill, Holetown, Barbados (photo courtesy of Simon Reader).

Chapter 1

Dunking behaviour in Carib grackles[1]

---

[1] Reprinted from Animal Behaviour, vol. 68, Morand-Ferron, J., Lefebvre, L., Reader, S. M., Sol, D. and Elvin, S., Dunking behaviour in Carib grackles, pp. 1267-1274, Copyright (2004), with permission from Elsevier.

Abstract

Dunking behaviour, the immersion of food items in water before consumption, has been anecdotally observed in over 30 species of birds in the wild, but its function and ecology have not been systematically studied. In experiments conducted in the field and in captivity on Carib grackles (*Quiscalus lugubris*) in Barbados, we demonstrated that (1) dunking rate in the field was influenced by food type and that moistening dry food seems to be one of dunking's major benefits; (2) most dunking observed in the field is performed by a minority of individuals, but the vast majority (86 %) of grackles tested in captivity were capable of dunking; (3) a higher density of conspecifics at a water source was associated with a lower dunking rate and an increased risk of kleptoparasitism when dunking; and (4) there were consistent individual differences in dunking and stealing frequency. We conclude that dunking is part of the normal behavioural repertoire of Carib grackles in Barbados, and that the low frequency of the behaviour in the field did not result from the incapacity of some individuals to perform the technique, but more likely from the balance of costs and benefits affecting its expression.

Introduction

Observers of animal behaviour are occasionally struck by foraging techniques that appear to be unusual, innovative, opportunistic and/or cognitively-sophisticated. When systematically collected, observations of this type have been useful in testing links between innovative cognition, neurobiology, ecology, and evolution in birds and primates (Reader & Laland 2002; 2003; Lefebvre et al. 2004). Dunking, the immersion of food in water before ingestion, is one technique that is mentioned in these observations. Over 30 bird species have been reported to dunk food in the wild (Table 1), often in contexts that suggest washing of soiled or toxic food, softening of hard or dry items, or smoothing the fur or feathers of hard-to-swallow prey. However, no study has yet documented individual rates of dunking, nor addressed experimentally the function of the behaviour.

In many cases, dunking seems to be performed by only a few individuals within a species and some observers suggest that putatively complex cognitive processes like insight (Pitochelli 1985) and social learning (Wible 1975) underlie the rare appearance of the technique. In contrast, others suggest that dunking might be part of the normal repertoire of entire genera like *Corvus* (Goodwin 1986) and *Quiscalus* (Jackson 1985). If this is the case, the rarity of observed dunking could be due to costs and benefits that apply to particular individuals and conditions. This situation would then be comparable to infrequent, but species-typical behaviour like bait-fishing in green-backed herons (*Butorides striatus*) or twig tool use in woodpecker finches (*Cactospiza pallida*). Higuchi (1988) and Tebbich et al. (2001) have shown that these techniques are more frequent in conditions where simpler foraging behaviours like passive waiting and foliage gleaning, respectively, are less efficient.

In the context of field and aviary experiments in Barbados, we witnessed dunking in a species in which the behaviour had not been previously reported, the Carib grackle (*Q. lugubris*). Carib grackles dunked food by walking with it to a water source, dropping it (often repeatedly) in the water, and retrieving it to be eaten immediately or flown away with. In captivity, three wild-caught grackles dunked fruit offered as part of a food neophobia test, and instances of bread-dunking in nearby rain puddles were observed during various field experiments. Some of the dunked pieces of bread were stolen by conspecifics at the moment of their release in the puddle (kleptoparasitism, reviewed by Brockmann & Barnard 1979). Enquiries to local ornithologists confirmed that dunking is occasionally observed in wild Carib grackles in different parts of Barbados (M. Frost, pers. comm.). *Q. lugubris* is very tame and opportunistic (ffrench 1991) and some aspects of its foraging behaviour and cognition have been well studied in the field in Barbados (Dolman et al. 1996; Lefebvre et al. 1997; Webster & Lefebvre 2001; Reader et al. 2002). The Carib grackle is thus an ideal species for field and captive studies on dunking.

In this paper, we characterize dunking rates in Carib grackles in the wild and examine the effects of food characteristics like dryness and dirtiness, as well as the effects of kleptoparasitism and conspecific density. In addition, we determine the individual propensities for dunking behaviour in the controlled, socially-isolated context of captivity, and we compare dunking rates in the same individuals in captivity and in the field. We also assess individual variation in dunking rate through observations of banded birds in the field. Our aim is to document individual variation and capacities for dunking, examine its proposed costs and benefits, and determine whether dunking is conditionally expressed according to local social conditions.

General Material and Methods

Study Area

The study was conducted in and around the grounds of the Bellairs Research Institute of McGill University, St. James, Barbados, from January to June 2002. Two of the four field sites (paved terraces: site A and B), drop traps, and the aviary used for captive experiments were situated on the grounds of the Bellairs Institute. The two other field sites were situated in Folkestone Park (site C and D), immediately to the south of Bellairs. All four sites were situated at least 50 m apart from one another.

Experimental Protocol

Each experiment involved offering either dry dog food pellets or cut pieces of bread. Bread is a regular food source for grackles in urbanised areas of Barbados (Dolman et al. 1996). The dog food pellets (0.7 cm in diameter, 21 % protein, Atlantic Marketing, Barbados) are readily eaten by grackles in captivity and in the wild, though they are apparently difficult to swallow. Ingestion could be facilitated by breaking the hard, dry pellets into pieces, but grackles' repeated pecking at the pellets was relatively inefficient at breaking the items.

In field experiments, the food was placed in a clump on the ground at a fixed distance from a consistently present, naturally-occurring puddle of water. Position and size (30 cm diameter) of the water puddle was kept constant during experiments by replenishment with tap water. The time of day and site of trials were randomised throughout the observation period.

Other bird species besides grackles took food items during experiments, but never dunked (pellets: *Zenaida aurita* and *Tyrannus dominicensis*; bread: *Z. aurita*, *T. dominicensis*, *Loxigilla noctis*, *Molothrus bonariensis*, and *Coereba flaveola*; see Reader et al. 2002). Our results deal only with the food items taken by *Q. lugubris*. Density counts of competitors at a site or a puddle considered only grackles.

Statistical Analysis

Testing the factors that influence the probability that a food item is dunked or stolen presents two statistical difficulties. First, data are unlikely to be independent, as they may be clustered both by trial and/or individual. For example, observations carried out within trials are likely to be more similar than those recorded among trials, as they are affected by similar conditions (location, weather, number of competitors, etc.). This clustering typically violates the assumption of data independence of standard statistical models. We dealt with this problem by using generalized linear models for autocorrelated data. In experiments 1 and 2, we specified a model with binomial error and logit link (PROC GENMOD in SAS version 8.01; Kuss 2002), in which the response variable was the proportion of the items taken by grackles in each trial that were dunked. This allowed us to test the influence of type of food on the probability that a food item was dunked, while accounting for the non-independence of food items from the same trial. When the response variable was binary (item is dunked or not, or stolen or not) we used generalized linear mixed models (%GLIMMIX macro in SAS version 8.01; Kuss 2002) with binomial error and logit link, including trial (experiment 2 and 3) and/or individual (experiment 3) as random factors. In both GLM approaches, multiple dunking or stealing on any one food item was considered as a single behavioural event. Whenever possible, we double-checked the results using traditional statistical tests (chi-square and sign test). In all cases, the conclusions of our analyses were identical.

The second difficulty is that even when we reduced the possible effects of pseudoreplication by statistically controlling for trial and individual, the link between response and explanatory variables may have been biased by their common correlation with a third variable. To control for the potential effect of some confounding variables, we included date, time, site, and density of competitors as co-variates in the models.

Experiment 1. Dunking rate in wild grackles

This experiment aimed to systematically document the prevalence of dunking behaviour in the field, and to see if food type influenced dunking rate.

Methods

In each trial, food pieces were presented near a puddle of water, and a single observer noted the response of birds taking food: 'fly away' with the food, drop it on the dry ground ('deposit'), or drop it in the puddle ('dunk'). A trial finished when no more food was available.

Seventy-one trials each involving 12 food items were performed on site A

(Seabourne flat, Bellairs). The first 20 trials used fresh white bread cubes (1 cm x 1 cm x 0.5 cm) placed on two cement columns situated 3 m and 6 m respectively from the water puddle. A second set of 20 trials used pellets of dry dog food. Two other sets of trials (17 trials with bread, 14 trials with pellets) were added to control for the possible carry-over effects of having the 20 trials with pellets follow the 20 trials with bread.

Results and Discussion

One to 12 grackles took the food on any one trial. The most frequent response to both bread and pellets was for a grackle to fly off with it to a tree (bread: 93.4 % of responses; pellets: 76.5 %). In comparison, dunking rate was very low: in only 65 out of 791 occasions did a grackle fly down from a column with a piece of bread or a pellet in its beak, walk to the puddle and dunk the food in it before eating the food on the spot or flying off with it in its beak (bread: 3.2 %; pellets: 13.6 %). In the remaining cases, a grackle flew down from the columns and deposited a food item on a dry part of the terrace (bread: 3.4 %; pellets: 9.9 %); the food was either then simply repositioned in the beak or attempts were made to break the item with the beak. That the observed dunking behaviour represents random dropping of the food is highly unlikely because the puddle covered less than 2 % of the terrace area and was the site of deposition of 56 % of items dropped by grackles. Furthermore, grackles walked directly and rapidly to the puddle with food in their beak and often deposited the item several times in the water. Pellets were both dunked in water and deposited on a dry part of the terrace more often than bread was (GENMOD, dunking: $X^2_1 = 12.29, p = 0.0005$; GENMOD, depositing: $X^2_1 = 13.71, p = 0.0002$). Intraspecific kleptoparasitic attempts occurred mostly when grackles were depositing items on the ground or when they were releasing food in the puddle in the course of dunking. In the latter cases ($n = 29$), only six attempts (20.7 %) resulted in successful kleptoparasitism.

This experiment demonstrated that dunking behaviour was rare in the field relative to simply flying away with the food, and that the type of food available could influence dunking rate. In the next experiment, we investigated further the influence of food type on dunking rate to examine possible benefits of the behaviour, and compare the rate of kleptoparasitism on dunked and non-dunked food.

Experiment 2. The context of dunking: softening, washing, and stealing

In this second field experiment, we tested two suggested functions of dunking behaviour (see Table 1) by comparing the rate of dunking of fresh versus dry bread, and of clean bread versus bread rolled in sand. If grackles dunk dry bread more often than fresh bread, this would suggest that they derive a benefit from softening dry and/or hard food. If grackles dunk sandy bread more often than clean bread, a washing benefit to the behaviour would be suggested. We also compared the rate of successful kleptoparasitism on dunked items versus non-dunked items; if dunked items tend to be stolen more often than non-dunked items, that would suggest that dunking behaviour exposes grackles to an increased risk of theft.

Methods

We compared dunking rate under two sets of food conditions: fresh versus dry bread (set 1), and clean versus sandy bread (set 2). For each of the two sets, a trial consisted of the presentation of one of the two food types near a puddle of water, and ended when all items had been eaten (or after 30 minutes). A single observer noted the duration of each trial, the maximum number of grackles at the site during each trial, the number of food items taken by grackles, and the rate of dunking, stealing bread and stealing dunked bread.

In each set, the two different food types were alternatively offered in pairs of trials (with less than 120 s between the two trials of a pair), with food type randomised with respect to order, time of day and site throughout the experimental period. We performed 144 trials at three sites (A, B, C). Each trial involved 50 pieces of one type of bread provided in a clump 1 m from the puddle. Each food piece was prepared from a 1 x 1 x 0.5 cm cube of fresh white bread. In the first set, fresh bread cubes were kept in a plastic bag up to the start of the experiment, whereas dry cubes were heated in an oven for 10 min at 52 °C. In the second set, both clean and sandy bread were moistened before a trial (10 ml of tap water per 50 cubes). Clean bread cubes were offered directly after moistening, while sandy bread cubes were rolled in 20 ml of sand after moistening.

Results and Discussion

In the first set, fresh bread was taken at a faster rate than dry bread, as evidenced by the shorter mean duration of the trials involving fresh bread (Mann-Whitney U test: $U = 946.5$, $n_1 = 36$, $n_2 = 36$, $p = 0.001$). Dunking rate was higher for dry bread than for fresh bread (6.4 % vs 3.4 % respectively, Fig. 2; GENMOD: $X^2_1 = 8.86$, $p = 0.0029$). In the second set, clean bread was taken at a faster rate than sandy bread (Mann-Whitney U test: $U = 312.5$, $n_1 = 36$, $n_2 = 36$, $p = 0.0001$), but dunking rate was not significantly different (2.9 % versus 2.8 %, Fig. 2; GENMOD: $X^2_1 = 0.21$, NS; power > 0.8, power estimate (Murphy & Mayors 1998) based on the effect size in the fresh-dry bread comparison and $\alpha = 0.05$). Thus, dunking behaviour was sensitive to food dryness and/or hardness, perhaps suggesting that grackles dunked to soften food. However, the coating of food with sand did not appear to alter dunking behaviour, providing no evidence that grackles derived a benefit from washing sandy food.

Kleptoparasitism was significantly more frequent on dunked food (14.6 %) than on non-dunked food (3.8 %; GLIMMIX, set 1: $F_{1,2465} = 74.72$, $p < 0.0001$; set 2: $F_{1,2610} = 107.78$, $p < 0.0001$), which suggests that dunking exposed grackles to an increased risk of theft. We could not record kleptoparasitic events occurring after grackles had flown away with food outside the limits of our observation site. However, we estimated the probability of this to be very low, as we never saw an aerial pursuit on a bird leaving with bread during these trials.

Experiment 3. Observations in the field and in captivity

In this set of experiments, we observed dunking behaviour in captive individuals, then released these individuals and made systematic field observations on them and on other free-ranging, individually-marked grackles. We presented both captive and free-ranging grackles with hard, dry food pellets near a water source in order to determine individuals' propensities to dunk (1) in isolation, where no kleptoparasitism is possible and no alternative food offered, and (2) in the field, where other feeding and behavioural options are available.

Thirty-six grackles were caught in baited drop traps, banded, and housed individually in aviaries for 10 days with ad libitum access to water. All birds were observed to eat some of the food pellets provided each day in two daily, 20 minutes sessions. Thirty-one (86 %) of these individuals were observed dunking. All birds were then released near their site of capture. We conducted field observations on the marked grackles at four sites in May and June 2002. In addition to the 36 birds studied in captivity, we had banded 124 wild grackles using unique combinations of coloured metal leg rings between February 2001 and May 2002. There was no significant relationship between individual dunking rates in captivity and in subsequent field observations (Pearson's regression: $F_{1,15} = 0.135$, NS). As the frequency distribution of dunking rate in individuals having been in captivity did not differ from that of grackles that had not been in captivity (Kolmogorov-Smirnoff, $X^2_2 = 0.273$, NS), and as released grackles did not dunk more in the field than the ones that had not been in captivity before (GLIMMIX: $F_{1,2142} = 0.336$, NS), we pooled all individuals for analysis.

Seventy-four recognizable individuals were observed more than three times in the field. Most of these birds showed either zero or very low rates of dunking, but approximately a quarter (18/74) showed rates varying between 25 % and 83.3 %, with an average dunking rate of 13 % (Fig. 3). The observed frequency distribution of dunking was tested against two theoretical distributions: one in which all birds dunked at the average 13 % rate (no specialisation) and one at which 13 % of the birds did all the dunking (complete specialisation). Tests of goodness of fit revealed that neither of the theoretical distributions accounted for the observed distribution in Fig. 3 (Kolmogorov-Smirnoff: $X^2_2 = 78.811$, $p < 0.0001$; $X^2_2 = 33.108$, $p < 0.0001$). Nevertheless, mixed-model analysis revealed consistent individual differences in dunking propensity, the variation in dunking rate among individuals being greater than the variation within individuals (GLIMMIX: $Z = 3.31$, $p = 0.0005$). We found no evidence that these differences were associated with sex (GLIMMIX: $F_{1,2142} = 1.88$, NS) or age (GLIMMIX: $F_{1,2142} = 0.69$, NS). We also found consistent individual differences in rate of stealing (GLIMMIX: $Z = 2.92$, $p = 0.0018$) as well as being stolen from (GLIMMIX: $Z = 2.11$, $p = 0.0173$).

Of the 74 individuals observed in the field, 46 were observed dunking, 28 stealing, and 30 were victims of kleptoparasitism. We could not analyse individual concordance between dunking, stealing and being stolen from within mixed-models, because the prevalence of the three behaviours was low compared to flying away with pellets. However, as is clear from Fig. 4a, 4b, and 4c, some birds showed all three behaviours, while others showed only one or none.

In the field, dunking rate showed a strong negative association with the density of grackles at the puddle (GLIMMIX: $F_{1,2142} = 18.61$, $p < 0.0001$). To further explore the effect of conspecific density on dunking and kleptoparasitic behaviours, we ran additional trials in which the food was placed in between two puddles of water spaced 4 m apart. We noted for each food item dunked the number of grackles present at both puddles and if the food item was stolen or not. Grackles dunked at the low-density puddle in 77 % of the 288 dunking observations in which there was a difference in conspecific density at the two puddles. In the few cases where grackles dunked at the high-density puddle, they were six times more likely to be kleptoparasitised than birds using the low-density puddle (GLIMMIX: $F_{1,490} = 19.54$, $p < 0.0001$).

General Discussion

Our experiments suggest that most, if not all, Carib grackles in Barbados are capable of dunking, but that the behaviour is conditionally expressed according to environmental and social conditions. Field experiments 1 and 2 demonstrated that the frequency of dunking was higher with hard, dry food than with soft, moist food. Thus, dunking appears to be a food processing technique that eases ingestion of dry and/or hard food through softening. However, we cannot exclude the alternative possibilities that (1) dry food promotes thirst, causing grackles to approach water at increased rates and so promoting dunking as a side-effect of their drinking behaviour or proximity to water (Heinrich 1999), or that (2) dry food acts as a better 'sponge' to aid water ingestion for the individual itself, or for its nestlings (Koenig 1985). Most grackles were observed eating dunked food on the spot, but as the breeding status of birds departing with dunked food was not known, we cannot reject the possibility that dunked food was given to nestlings; indeed, one free-ranging female was observed dunking bread and feeding it to a nearby juvenile in February 2002. If the food is used as a sponge during dunking, then the behaviour would be an example of tool use (see van Lawick-Goodall 1970; Beck 1980; McFarland 1982; Lefebvre et al. 2002). Despite the fact that almost all the sand covering the bread in experiment 2 could be quickly removed by dunking, grackles did not dunk sandy bread more often than clean bread. Thus, washing of sand-covered food does not appear to be an important function of dunking in *Q. lugubris*. Other food characteristics may however elicit the behaviour. For example, captive grackles dunked sticky maraschino cherries (S. M. Reader, pers. obs.).

Social context also seemed to influence the frequency of the behaviour. Dunking rate was negatively associated with conspecific density at the puddle (experiment 3). Higher grackle densities were also associated with an increased risk of kleptoparasitism when birds could dunk at one of two puddles, and birds generally dunked at the puddle with lower conspecific densities. Costs associated with the potential theft of food items (wasted time and energy, lost opportunities for energy and nutrients, risk of injuries, etc.) may have influenced grackles' use of dunking behaviour, as dunking seemed to expose them to an increased risk of kleptoparasitism (experiment 2). A similar observation has been made by

Visalberghi & Fragaszy (1990) on one *Macaca fascicularis* that was kleptoparasitised by conspecifics when dunking sandy fruits in captivity; the female dunked more often when conspecifics were away from the water source.

Our results indicate that the low frequency of an apparently complex foraging technique need not indicate that only a few individuals are capable of its performance. To address this issue, individuals need to be tested under conditions favourable to the expression of the behaviour (e.g. Drea & Wallen 1999), but still have the option of not performing it. In our study, aviary conditions were favourable to dunking, i.e. hard, dry food near water, with no risk of kleptoparasitism, but grackles could still feed by swallowing the pellets whole. If a majority of individuals show the technique in favourable conditions, as grackles did here, the rarity of the behaviour in normal field situations may result from variation in the costs and benefits experienced by individuals in different situations, rather than an inability to perform the technique. Tebbich et al. (2002) have shown that woodpecker finches frequently use twig tools in the wild in arid habitats, but very rarely do so in humid ones. In captive conditions where tool-use was encouraged by hiding food in slits, however, wild-caught juvenile finches developed tool-use, whether they were from arid habitats or more humid ones (Tebbich et al. 2001). Many behaviour patterns will be sensitive to prevailing conditions, the efficiency of alternative techniques, and the (possibly frequency-dependent) balance of costs and benefits for a particular individual. The rare performance of a behaviour pattern need not suggest that performers possess unusual capacities compared to their conspecifics.

Our results do not rule out the possibility that dunking was produced *de novo* by each individual in captivity. However, the finding that a majority of our Carib grackles dunked at least once in the field (33 out of 57 wild grackles that had not been in captivity before), added to the fact that five out of the six *Quiscalus* species have now been reported to dunk (*Q. quiscula*, *Q. mexicanus* and *Q. major*, see Table 1; *Q. lugubris*, this study; *Q. niger*, A. S. Griffin, pers. comm.; no record for *Q. nicaraguensis*), support Jackson's (1985) suggestion of a possible generalised propensity to dunk in this genus.

Acknowledgements

We are grateful to Éric Trottier and Martin Frost for their help in the field, and to Luc-Alain Giraldeau for comments on a previous version of the paper. Funding for this work was provided by an NSERC grant to L.L. and an NSERC postgraduate scholarship to J.M.F. The study was conducted under McGill University Animal Use Protocol #4519.

References

Banks, S. 1982. Grey heron dunking and swallowing large rat. British Birds, 75, 181.

Beck, B. B. 1980. Animal tool behavior: the use and manufacture of tools by animals. New York: Garland.

Bent, A. C. 1958. Life histories of North American blackbirds, orioles, tanagers, and allies. U. S. National Museum Bulletin, 211, 395-421.

Bowey, K. 1997. Grey heron catching common starling in flight. British Birds, 90, 112-113.

Brampton, A. H. 1994. Carrion crow dunking nuts. British Birds, 87, 478.

Brockmann, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. Animal Behaviour, 27, 487-514.

Caldwell, J. A. 1951. Food-washing in the water-rail. British Birds, 44, 418.

del Hoyo, J., Elliott, A. & Sargatal, J., Eds. 1996. Handbook of the birds of the world, vol. 3. Barcelona: Lynx Edicions.

Dolman, C. S., Templeton, J. & Lefebvre, L. 1996. Mode of foraging competition is related to tutor preference in *Zenaida aurita*. Journal of Comparative Psychology, 110, 45-54.

Drea, C. M. & Wallen, K. Low-status monkeys "play dumb" when learning in mixed social groups. Proceedings of the National Academy of Sciences of the United States of America, 96, 12965-12969.

ffrench, R. 1991. A guide to the birds of Trinidad and Tobago. New York: Cornell University Press.

Goodwin, D. 1986. Crows of the world. 2nd edn. England: British Museum.

Hauri, R. 1956. Beitrage zur biologie des kolkraben (*Corvus corax*). Ornithologische Beobachtungen, 56, 28-35.

Heinrich, B. 1999. Mind of the raven. New York: Harper Collins.

Henry, P.-Y., Bénéat, Y. & Maire, P. 1998. Redshank *Tringa totanus* feeding on young edible frogs *Rana kl. esculenta*. Nos Oiseaux, 45, 57-58.

Higuchi, H. 1988. Individual differences in bait-fishing by the green-backed heron associated with territory quality. Ibis, 130, 39-44.

Jackson, J. 1985. The dunking habit of common grackles. American Birds, 39, 261-262.

Johnson, I. W. 1976. Washing of food by spotless crake. Notornis, 23, 357.

Jones, C. G. 1979. Birds dunking food. British Birds, 72, 189-190.

Jordheim, S. O. 1965. Unusual feeding behaviour of yellowlegs. Blue Jay, 23, 25.

Koenig, W. D. 1985. Dunking of prey by Brewer's blackbirds: a novel source of water for nestlings. Condor, 87, 444-445.

Kuss, O. 2002. How to use SAS for logistic regression with correlated data. Proceedings of the 27th Annual SAS Users Group International Conference (SUGI 27), 261-27.

Lefebvre, L., Templeton, J., Brown, K. & Koelle, M. 1997. Carib grackles imitate conspecific and Zenaida dove tutors. Behaviour, 134, 1003-1017.

Lefebvre, L., Nicolakakis, N. & Boire, D. 2002. Tools and brains in birds. Behaviour, 139, 939-973.

Lefebvre, L., Reader, S. M. & Daniel Sol. 2004. Brains, innovations and evolution in birds and primates. Brain Behavior and Evolution, 63, 233-246.

Luchtemeyer, E. A. 1969. Unusual behavior of robin, *Turdus migratorius*, and red-winged blackbirds, *Agelaius phoenicus*. Florida Naturalist, 42, 135.

McFarland, D. 1982. The Oxford companion to animal behaviour. Oxford: Oxford University Press.

McMillan, M. 1992. How to feed muppets - soak the bones! Bird Observer (Nunawading), 12, 726.

Murphy, K. R. & Myors, B. 1998. Statistical power analysis: a simple and a general model for traditional and modern hypothesis tests. New Jersey: Laurence Erlbaum Associates.

Nicklas, B. 1974. Bird behavior. Chat, 38, 88.

Nimmo, C. E. Jr. 1970. Birds and water. Raven, 41, 59-63.

Otnes, G. 1977. Unusual feeding behavior of a great blue heron. Loon, 49, 233.

Pitochelli, J. 1985. Apparent insight learning by some common grackles breeding in Central Park, New York. Kingbird, Winter, 32-33.

Pulich, W. M. 1969. Unusual behavior of three species of birds. Wilson Bulletin, 81, 472.

Purser, G. L. 1959. House sparrows soaking hard bread to soften it. British Birds, 52, 199-200.

Radford, A. P. 1979. Starling eating feather. British Birds, 72, 188.

Rand, A. L. 1967. A common grackle learning to soak bread. Wilson Bulletin, 79, 455-456.

Reader, S. M. & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences of the United States of America, 99, 4436-4441.

Reader, S. M. & Laland, K. N., Eds. 2003. Animal innovation. Oxford: Oxford University Press.

Reader, S. M., Morand-Ferron, J., Côté, I. & Lefebvre, L. 2002. Unusual feeding behaviors in five species of Barbadian birds. El Pitirre, 15, 117-123.

Seibt, U. & Wickler, W. 1978. Marabou storks wash dung beetles. Zeitschrift fur Tierpsychologie, 46, 324-327.

Schardien, B, J. & Jackson, J. A. 1982. Killdeers feeding on frogs. Wilson Bulletin, 94, 85-87.

Simmons, K. E. L. 1950. Food-washing by common sandpiper. British Birds, 43, 229-230.

Stokes, D. & Stokes, L. 1985. Bird song (Part II). Bird Watcher's Digest, 7, 54-59.

Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. 2001. Do woodpecker finches acquire tool-use by social learning? Proceedings of the Royal society of London Series B-Biological sciences, 268, 2189-2193.

Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M. 2002. The ecology of tool-use in the woodpecker finch. Ecology Letters, 5, 656-664.

Vader, W. 1979. Cleptoparasitism on bar-tailed godwits by common gulls. Fauna, 32, 62-65.

Van Lawick-Goodall, J. 1970. Tool-using in primates and other vertebrates. Advances in the Study of Behaviour, 3, 195-249.

Visalberghi, E. & Fragaszy, D. M. 1990. Food-washing behaviour in tufted capuchin monkeys, *Cebus apella*, and crabeating macaques, *Macaca fascicularis*. Animal Behaviour, 40, 829-836.

Watkin, R. 1950. Food-washing by blackbird. British Birds, 43, 156.

Webster, S. J. & Lefebvre, L. 2001. Problem solving and neophobia in a columbiform-passeriform assemblage in Barbados. Animal Behaviour, 62, 23-32.

Wible M. W. 1975. Food washing by grackles. Wilson Bulletin, 87, 282-283.

Zach, R. 1979. Shell dropping: decision-making and optimal foraging in Northwestern crows. Behaviour, 68, 106-177.

Table 1. Reports of dunking behaviour in free-ranging birds.

Species	Items dunked	Reported context	Source
Agelaius phoenicus	Bread, crackers	.	Luchtemeyer 1969
Ardea cinerea	Large dead rat	1	Banks 1982
	Dead starling	1	Bowey 1997
Ardea herodias	Common gopher	1	Otnes 1977
Calidris alpina	Worms	2	del Hoyo et al. 1996
Calidris ferruginea	Worms	2	del Hoyo et al. 1996
Charadrius vociferus	Frogs	2	Schardien & Jackson 1982
Corvus caurinus	Broken whelks	2	Zach 1978
Corvus corax	Carrion	.	Jones 1979
Corvus corone	Hard, dry bread	1	Jones 1979
	Hard crusts of bread, jammy pastry	1, 2	Goodwin 1986
	Nuts	.	Brampton 1994
Corvus mellori	.	.	McMillan 1992
Corvus splendens	Hard crusts of bread	1	Goodwin 1986
Euphagus cyanocephalus	Grasshoppers	3	Koenig 1985
Larus delawarensis	Cheese crackers	.	Stokes & Stokes 1985
Leptoptilos cruminiferus	Dung beetles	2	Seibt & Wickler 1978
Limosa lapponica	Lugworms	2	Vader 1979
Limosa limosa	.	2	del Hoyo et al. 1996
Passer domesticus	Hard, dry bread crusts	1	Purser 1959
Porzana tabuensis	Caterpillar	2	Johnson 1976
Quiscalus lugubris	Dry dog food, bread, maraschino cherries	1	This study
Quiscalus major	Bread	1	Wible 1975
	Dry dog food	1	Jackson 1985
Quiscalus mexicanus	Dry dog food, bread, insects, table scraps	1	Pulich 1969
	Pecans, table scraps	1	Stokes & Stokes 1985
Quiscalus niger	.	.	A. S. Griffin, pers. comm.
Quiscalus quiscula	Bread, crackers	1	Bent 1958
	Dry bread	1	Rand 1967
	Bread	.	Luchtemeyer 1969
	Dry bread	.	Nimmo 1970
	Dry bread	1	Nicklas 1974
	Bread, mulberry, cricket, peanuts, fruits	1, 2	Wible 1975
	Bread, dried pastry	1	Jackson 1985

	Stale bread, pizza crust, crackers	1, 3	Pitocchelli 1985
Rallus aquaticus	Food picked up deep in mud	2	Caldwell 1951
Sturnus vulgaris	Feather	.	Radford 1979
Tringa hypoleucos	Food probed from the mud	2	Simmons 1950
Tringa melanoleuca	Crickets	2	Jordheim 1965
Tringa totanus	Frogs	2	Henry et al. 1998
Turdus merula	Leather-jackets	2	Watkin 1950

Context (as suggested in the source): 1 = softening or soaking; 2 = washing; 3 = water for nestlings. We excluded reports for birds kept in captivity and cases of drowning of live prey.

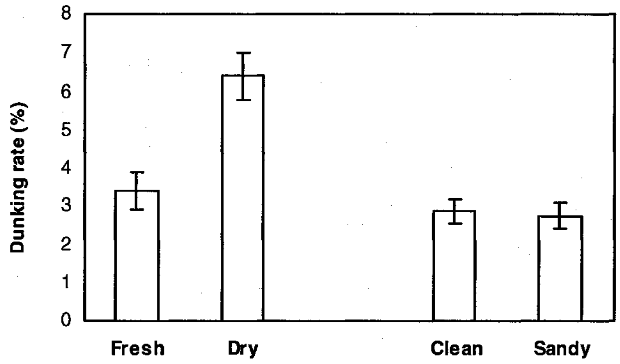

Fig. 2. Dunking rate (percentage of items taken that were dunked, ± SE) of fresh and dry bread, and of clean and sandy bread.

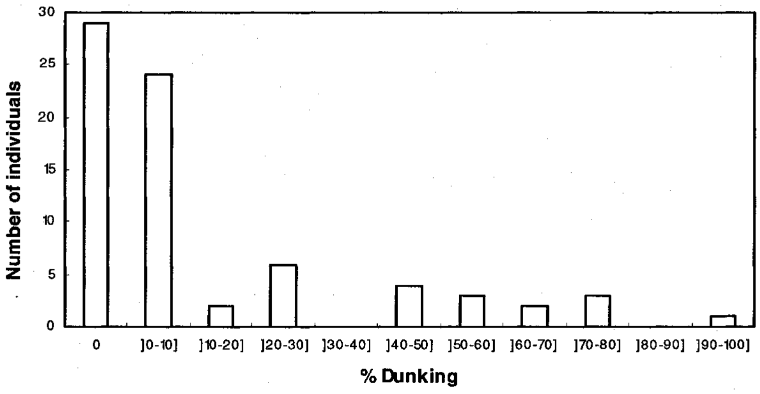

Fig. 3. Observed frequency distribution of dunking (percentage of behavioural events that were dunking events) in the field.

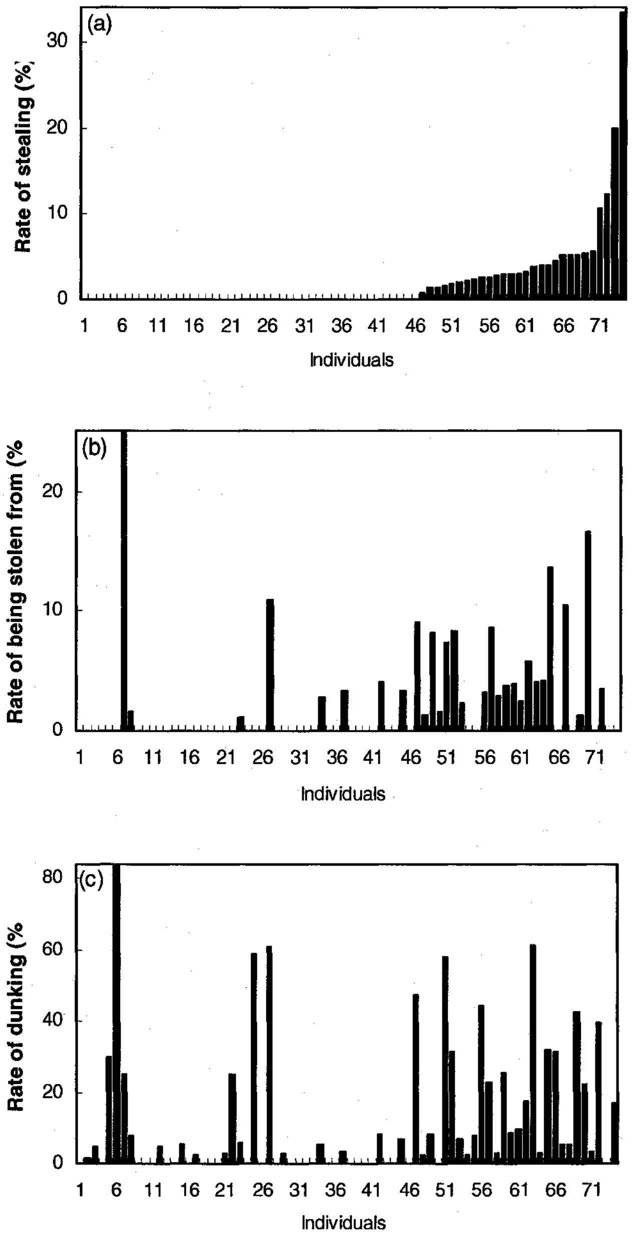

Fig. 4. Individual rates of (a) stealing, (b) being stolen from, and (c) dunking, expressed as percentages of the total number of behavioural events. Individuals occupy the same position on the x axis of all three graphs, and are sorted by increasing rate of stealing (a).

In the previous chapter, I reported on a foraging innovation: dunking behaviour in Carib grackles of Barbados. I described rates of expression of the behaviour in the field and in captivity, and concluded that the low rates of dunking observed in the field are probably not due to the limited ability of individuals to learn and/or perform dunking, as evidenced by the large proportion (86 %) of individuals exhibiting the behaviour in captivity, but more probably to the balance of costs and benefits of dunking versus that of alternative foraging tactics. I tested two potential benefits of dunking, soaking and washing, and found that grackles dunked dry food more often than fresh food, suggesting that dunking might be a food-processing behaviour easing the ingestion of hard and dry items. The increased probability of kleptoparasitism when dunking food than when feeding on similar items but not engaging in dunking pointed at losses to conspecifics as an important cost to dunking. In this chapter, I further explore the function of dunking behaviour by comparing handling time in birds eating dry versus dunked items. Then, I examine some determinants of kleptoparasitic host selection in order to understand why dunking birds were robbed of food more often than non-dunking birds, and I discuss kleptoparasitism as a factor limiting the expression of tool-related behaviours. I also document the use of two tactics used flexibly by grackles that allowed reducing losses to kleptoparasites when dunking.

Chapter 2

Stealing of dunked food in Carib grackles (*Quiscalus lugubris*)[1]

---

[1] Reprinted from Behavioural Processes, vol. 73, Morand-Ferron, J., Veillette, M. and Lefebvre, L., Stealing of dunked food in Carib grackles (*Quiscalus lugubris*), Copyright (2006), with permission from Elsevier.

Abstract

The use of tool or tool-like food processing behaviours can render animals vulnerable to theft (kleptoparasitism) because (1) large, nutritious items are usually involved, (2) value is added to the food due to long and/or complex handling, and (3) physical control of items is often temporarily lost during handling. In Barbados, Carib grackles (*Quiscalus lugubris*) immersing items in water before consumption (a behaviour known as food dunking) lose a larger proportion of items to conspecific food thieves than grackles that do not dunk. In this paper, we first show that dunking in Carib grackles functions as a food-processing technique that speeds up ingestion. We then examine five potential predictors of kleptoparasitism: only conspecific density and loss of physical control on food were found to influence the probability that birds would be attacked and successfully robbed of food by conspecifics. Grackles could reduce the probability of kleptoparasitism by holding items in the bill while dunking and engaging in head-up displays. These behaviours were used flexibly depending on variation in the risk of kleptoparasitism. We suggest that costs like the ones incurred from theft might limit the profitability and frequency of tool and proto-tool food processing behaviours, creating a context where counter-strategies might be selected.

Introduction

Foragers can exploit the searching and handling efforts of others by engaging in food-stealing, or kleptoparasitism (Brockmann & Barnard 1979). Any situation that lengthens handling or reduces control over high-quality food items may increase the benefits of parasitic tactics in a population (Giraldeau and Caraco 2000). The use of environmental features to modify or manipulate food might be one of these situations: when a gull drops a shell on a hard substrate (e.g. Norris et al. 2000) or a macaque uses water to separate wheat grains from sand (Kawai 1965), it becomes vulnerable to exploitation by competitors. This potential "scrounging cost" has not been recognised in explaining the low frequency of tool, proto-tool (Parker & Gibson 1977) and other food processing behaviours in wild animal populations, although it has been observed previously that some individuals will refrain using a tool or proto-tool in the presence of potential kleptoparasites (e.g. Visalberghi & Fragaszy 1990). Here, we focus on dunking, a processing technique used by several species of grackles (Jackson 1985) and corvids (Goodwin 1986) and examine the factors affecting vulnerability and the counter-tactics of dunkers faced with the risk of intraspecific kleptoparasitism.

Our study species is the Carib grackle (*Quiscalus lugubris*), a generalist passerine that feeds in groups on high-quality, clumped food resources (mostly anthropogenic) in urban areas of Barbados (Jaramillo & Burke 1999). Carib grackles occasionally engage in dunking behaviour, the immersion of food items in water before consumption (Morand-Ferron et al. 2004; see Hickey 2005 for a photograph). Previous field observations have revealed that dry food items elicit a higher frequency of dunking than fresh items, raising the possibility that dunking facilitates the consumption of food types that are hard to ingest. In the first part of this paper, we provide evidence that dunking accelerates food ingestion and is thus an advantageous processing behaviour in this population. In the second part, we test the effects of sex, age and density of conspecifics on kleptoparasitism, as well as item profitability and loss of physical control over food. Finally, we examine whether potential hosts can respond flexibly to variation in the risk of kleptoparasitism and we describe two strategies employed by hosts to reduce their losses.

A. Does dunking help grackles to process food?

Dunking behaviour has been reported in more than 30 bird species in the wild (see table 1 in Morand-Ferron et al. 2004). It has been suggested to serve at least four different potential functions: use of water to wash food (e.g. marabou storks *Leptoptilos crumeniferus* washing dung beetles; Seibt & Wickler 1978), soften hard items (e.g. house crow *Corvus splendens* softening dry bread; Jones 1979), drown live prey (e.g. Eurasian sparrowhawk *Accipiter nisus* drowning Eurasian jay *Garrulus glandarius*; Weekley 1997), or use of food as a sponge to transport water to nestlings (e.g. Brewer's blackbird *Euphagus cyanocephalus*; Koenig 1985). In the first three cases, dunking is among the techniques that Parker and Gibson (1977) would classify as proto-tool use, in which the environmental feature that functions as a tool (water) is not detached from the substrate or held by the animal. Only in the last case would dunking be considered a true tool behaviour (Beck 1980; Lefebvre et al. 2002), where the environmental feature is detached and manipulated by the user. In free-ranging Carib grackles, previous work suggests that dunking might ease the ingestion of items that are difficult to swallow (Morand-Ferron et al. 2004). If Carib grackles derive some food processing benefits from dunking items in water, we predict handling and consumption times to be shorter with dunked items than they are with dry ones.

Mis en forme

Mis en forme

Mis en forme

Mis en forme

Mis en forme

Material and methods

This experiment was conducted at three different field sites in the parish of St. James, Barbados: (1) the paved terrace of Seabourne residence, located in the grounds of the Bellairs Research Institute of McGill University; (2) Folkestone Park, located to the immediate south of Bellairs; and (3) a public parking lot in Holetown, located ca. 1km south of Folkestone.

At the beginning of each session, the observer (J.M.F.) placed ca. 100 dry dog food pellets (0.7 cm in diameter, 21% protein, Atlantic Marketing, Barbados) in a clump on the ground 1 m from a naturally occurring puddle of water. Dry dog food pellets are readily eaten by grackles in captivity and in the wild, even though they are difficult to swallow and need to be broken in smaller pieces through repeated pecking (Morand-Ferron et al. 2004). Each time a bird took a food item, the observer (if not already watching another individual) noted the time this individual took: (1) to first deposit the item on the ground, in the water, or on a perch in a tree (travel time); and (2) to swallow the item completely (total time). The observer also noted the behaviour of the individual, using the following categories: eat dunked item, eat dry item while on the ground, eat dry item while perched in a tree. For this experiment, we excluded cases where the individual lost its item to a kleptoparasite or abandoned it without successfully feeding on it. We used two different measures of handling time: total time and consumption time (total time minus travel time). After log transformations, these data were normally distributed and we performed a one-way ANOVA and Tukey post-hoc comparisons to compare total time and consumption time of the three different behavioural categories observed. The results are similar for the two time measures and we thus present results for consumption time only, as travel time is comparatively short (mean travel time ± sd is 12.0 ± 12.1 s compared with 166.8 ± 176.6 s for consumption time) and depends on the experimental placement of food and water in the case of dunking.

As not all birds observed in this experiment were marked (Carib grackles feed in open flocks with frequent changes in composition; see also Morand-Ferron et al. 2004), it is possible that some birds might have been observed more than once. We consider however that we reduced this possibility by performing observations at three different field sites, using individuals that had leg bands only once each (21 individually-recognisable birds over a total of 74 observations), and switching between males and females and adults and juveniles whenever possible between observations in the same session (for a total of 20 sessions).

Results

We found a significant effect of the type of behaviour on consumption time (ANOVA: $F_{2, 71} = 20.4, p < 0.001$; fig. 5). Consumption time was two to three times shorter after dunking food in water than when consuming dry items on the ground (Tukey; $p < 0.001$) or while perching in a tree (Tukey; $p = 0.003$). There was no difference in consumption time when eating dry items on the ground or in a tree (Tukey; $p = 0.99$).

These results suggest that one benefit of dunking is reduced handling time, thereby providing support for the food processing function of this behaviour in Carib grackles.

B. Why are dunked items more often stolen than dry ones?

In a previous study (Morand-Ferron et al. 2004), we observed that 13% of items that were dunked were lost to kleptoparasites, while only about 2% of items that were taken from the same food pile but not dunked were similarly lost. This difference could be due to many factors; from the results of the previous section, one could predict that, all other things being equal, kleptoparasites would preferentially target dunked items over dry ones, as dunked items require shorter handling times. In order to isolate the effect of item profitability from other variables, we compare the probability of kleptoparasitic attempts on dunked items versus dry items deposited on the ground at the same site. We predict more attempts on dunked than on dry items.

One reason dunking birds are more often victims of kleptoparasitism could be that they are manipulating food items at the water puddle, where there may be a greater build-up of birds (drinking, bathing, waiting for stealing opportunities, etc.) than in surrounding areas. Here, we compare conspecific density around focal birds handling a dunked item at the puddle versus birds manipulating a dunked item away from the puddle. We predict density to be higher at the water puddle, and to be significantly correlated with the probability of kleptoparasitic attempts and success.

The existence of two distinct dunking techniques in Carib grackles allows us to examine the effect of loss of physical control on food on the probability of kleptoparasitic attempts and success, while keeping item profitability constant. Grackles dunk by either releasing and retrieving an item from water (release technique) or by dipping an item in water while holding it in the bill (hold-while-dunking technique). We predict a higher probability of kleptoparasitic attempts and success on items dunked using the release technique compared to items held in the bill during dunking.

Sex and age biases in kleptoparasitic losses have been observed in many species, often with the subordinate sex or age class being preferentially robbed of food (e.g. Burger & Gochfeld 1981; Ens et al. 1990). Assuming that males are dominant over females and adults over juveniles in Carib grackles (from what is known on other *Quiscalus* species; Post et al. 1996; Johnson & Peer 2001), we predict a higher probability of kleptoparasitic attempts and success on females than on males and on juveniles than on adults.

To summarize, we predict more kleptoparasitism (1) at higher conspecific density, (2) on dunked items rather than dry items deposited on the ground (item profitability), (3) on items released in water than on items held in the bill while dunking (loss of physical control on food), (4) on females than on males, and (5) on juveniles than on adults.

Material and methods

The experiment was conducted on Seabourne terrace. Approximately 100 food pellets (see section A) were placed in a clump on the ground 1 m from a naturally-occurring puddle of water, modified to achieve a constant size (50 cm in diameter) and water depth (2 cm) by replenishing it with tap water and lining it with plastic sheeting. The food pile and water puddle were replenished before each session and during a session if they were to be half-depleted. A similar experimental setting had already been in place for other field experiments in the seven weeks preceding this study.

We performed opportunistic focal observations of grackles taking food pellets from the pile and manipulating them on the ground. All observations were recorded using a digital camcorder. An observer (M.V.) noted verbally on the videocassettes the number of times that each focal bird deposited a dry item on the ground, dunked an item in water through release and retrieval, dunked while holding the item in the bill or deposited a dunked item on the ground. The observer also noted the sex and age category (adult or juvenile; Jaramillo & Burke 1999) of the focal individual, the number of aggressive displays it performed, whether the bird was subject to kleptoparasitic attempts, and whether or not these attempts were successful. Kleptoparasitic acts consisted of rapid movements of a grackle towards a food item handled by a focal individual, which, when successful, ended with the kleptoparasite gaining possession of the item. A second observer (J.M.F.) doubled-checked the data while scoring videorecordings and counted the number of grackles within a 15 cm radius of the focal individual for each act. We conducted 35 observational sessions of 30 minutes each, for a total of 4149 acts recorded.

As a grackle could engage in different behaviours with a single item, we had to analyse our data at the level of acts, not individuals or food items. Such data will not be statistically independent. To overcome this difficulty, we used generalised linear mixed models for autocorrelated data (%GLIMMIX in SAS version 8.2; Kuss 2002) with binomial error and logit link, including day, session and item as random nested factors. We examined the significance of one variable at a time in explaining the occurrence or absence of kleptoparasitic attempts (either missed or successful) and success. The null hypothesis was rejected when there was a significant deviation from chance; because we tested five hypotheses using the same data, we applied Bonferroni corrections throughout, setting the level for significance at 0.01 for each test (Stevens 2002).

Results

We recorded a total of 4149 acts on 922 items manipulated on the experimental site by focal birds. Of those acts, 11.3 % consisted in depositing a dry item on the ground ($n = 470$), 24.8 % in depositing a dunked item on the ground ($n = 1030$), 50.7 % in dunking an item using the release technique ($n = 2104$) and 13.1 % in using the dunk hold technique ($n = 545$). The average rate of kleptoparasitic attempts (unsuccesful and successful) on all acts was 10.8 %, with 32.6 % of these attempts ending in successful stealing events. Figure 6 shows the proportion of unsuccessful and successful kleptoparasitic attempts on each of the four types of foraging behaviour.

Conspecific density

Grackles manipulating food at the water puddle were surrounded by a larger number of conspecifics than those handling a dunked item on a dry part of the site (2.14 ± 0.9 versus 1.44 ± 0.7, respectively; GLIMMIX: $F_{1,3217} = 276.6$, $p < 0.001$). In general, the number of conspecifics within 15 cm of a focal individual was positively correlated with kleptoparasitic attempts (GLIMMIX: $F_{1,3583} = 199.3$, $p < 0.001$) and success (GLIMMIX: $F_{1,3583} = 84.9$, $p < 0.001$). In order to control for this confounding effect, we included grackle density counts in all subsequent analyses.

Item profitability

Contrary to our prediction, there were no significant differences in kleptoparasitic attempts or success on dry versus dunked items when both food types were deposited on the ground (11.3 % attempts on dry items versus 12.7 % on dunked items: GLIMMIX: $F_{1,1062} = 0.99$, $p = 0.319$; 5.7 % successes on dry items versus 3.7 % on dunked items: GLIMMIX: $F_{1,1062} = 0.98$, $p = 0.322$). Once picked up, however, dry pellets were abandoned more often than dunked ones (6.4 % versus 0.1 %, respectively; Chi-square: $\chi^2_1 = 352.5$, $p < 0.001$).

Loss of physical control on food

As predicted, attempts were more frequent on items released during dunking than on items held in the bill (12.7 % versus 4.4 %, respectively: GLIMMIX: $F_{1,2288} = 46.8$, $p < 0.001$); success rate was also higher for the former (4.5 % successes on items released in water versus 0.9 % on items held in the bill: GLIMMIX: $F_{1,2287} = 26.5, p < 0.001$).

Sex and age category

Females and males were targeted and victimised equally often (attempts: GLIMMIX: $F_{1,3582} = 0.96, p = 0.327$; successes: GLIMMIX: $F_{1,3582} = 0.01, p = 0.922$). We did not detect a significant difference between the probability of juveniles and adults being attacked (GLIMMIX: $F_{1,3582} = 0.75, p = 0.387$) and successfully robbed of food by kleptoparasites (GLIMMIX: $F_{1,3582} = 3.09, p = 0.079$). We obtained similar results when controlling for the behaviour performed by focal individuals (sex, attempts: GLIMMIX: $F_{1,3577} = 0.86, p = 0.353$; sex, successes: GLIMMIX: $F_{1,3579} = 0.01, p = 0.956$; age, attempts: GLIMMIX: $F_{1,3579} = 1.60, p = 0.206$; age, successes: GLIMMIX: $F_{1,3579} = 3.92, p = 0.048$).

To summarize, we observed more kleptoparasitism at higher conspecific density, and on items released in water than on items held in the bill while dunking, but found no significant effect of item profitability, sex or age of hosts (juveniles tended to be successfully robbed of food more often than adults, but this effect was not significant when applying Bonferroni's correction).

C. How to reduce losses to kleptoparasites?

In the previous section, we showed that dunking grackles could reduce their losses to conspecifics by holding food pellets in the bill while dunking. Paradoxically, grackles used the hold technique four times less frequently than the release technique (the latter accounted for 79.4 % of dunks). If the safer, but less common hold-while-dunking technique involves additional costs with respect to the release technique, grackles should hold food items in the bill mostly when the risk of kleptoparasitism is high. We thus predict focal individuals to use the hold technique when surrounded by a larger number of conspecifics than when using the release technique.

When competing for food, both male and female Carib grackles sometimes engage in aggressive head-up displays, in which the bill is raised at an elevation of about 45° and the grey nictitating membrane is drawn briefly over the eyes (Wiley 1975). We predict grackles to engage in more numerous displays when they are the targets of more numerous kleptoparasitic attempts. We also predict that grackles using these displays will successfully reduce the risk of losing items to food thieves.

Material and methods

The prediction on dunking techniques was tested using the data and methods of section B. The predictions on displays were tested on the trials used in section B and on a third set of field experiments conducted in very similar conditions, but with the camcorder zoomed in more closely on focal individuals. We pooled these trials with the ones analysed in the previous section (for a total of 3941 items) after we ascertained that there was no significant confounding effect of data source (GLIMMIX: $F_{1, 3881} = 1.19$, NS). We tested the effect of the number of displays per item dunked on the probability of kleptoparasitic attempts and success using generalised linear mixed models with binomial error and logit link, including data source, day and session as random nested factors, and conspecific density as a fixed effect.

Results

In comparison with the release technique, the hold-while-dunking technique was performed when focal birds were surrounded by a larger number of conspecifics (on average, 2.09 ± 0.9 conspecifics versus 2.28 ± 1.0, respectively; GLIMMIX: $F_{1, 2289} = 18.8$, $p < 0.001$; fig. 7). Including the hold technique in the dunking process significantly increased handling time compared with releasing items only (52.4 ± 23 s versus 44.8 ± 21 s, respectively; Two-sample t-test: $t_{156} = -2.21$, $p = 0.028$). The hold technique did not seem to be restricted to a small part of the population as 17 out of the 23 (73.9 %) banded birds observed dunking in this study engaged in both the release and hold-while-dunking technique, sometimes using the two techniques in manipulating a single item.

As predicted, focal individuals receiving more kleptoparasitic attacks engaged in more head-up displays per item (GLIMMIX: $F_{1,3881} = 20.2$, $p < 0.001$). Birds engaging in more displays per dunked item significantly reduced their probability of being robbed of food by kleptoparasites (GLIMMIX: $F_{1,3881} = 7.3$, $p = 0.007$).

These results suggest that holding items in the bill while dunking and engaging in head-up displays are efficient anti-kleptoparasitic tactics in Carib grackles.

Discussion

Our finding that dunked items could be ingested more quickly (including the time spent dunking) than dry ones is consistent with the idea that dunking is a food processing behaviour easing the ingestion of items that are difficult to swallow. Dunking is included in proto-tool behaviours by Parker and Gibson (1977), as the animal uses an element of the environment (water) to modify the characteristics of a resource (food). Animals making use of a proto- or a true tool may suffer greater kleptoparasitic losses compared with individuals engaged in other foraging behaviours on similar items, but there have been very few attempts to make this comparison in the field. In order to examine why dunking birds were robbed of food more often than non-dunking birds (Morand-Ferron et al. 2004), we tested five potential predictors of kleptoparasitism in free-ranging grackles. We found that dunking birds were more often kleptoparasitised because (1) they manipulated items at the water puddle where the density of conspecifics, and thus the risk of kleptoparasitism, was high, and (2) they released items from the bill during handling. Birds eating dry items have the possibility of flying directly into trees where they usually perch without any conspecific in close proximity (Morand-Ferron, pers. obs.); dunking can thus be considered more risky as it involves manipulating the item at the water puddle.

We did not find an effect of sex or age of the host, nor of increased item profitability on kleptoparasitic occurrence. Surprisingly, kleptoparasites did not preferentially target dunked items over dry items, despite the observation that dunked items could be swallowed more quickly and that grackles seemed to value dry items less than dunked ones (dunked items were abandoned far less often than dry items). The most probable explanation for this lack of preference is that kleptoparasites could not distinguish visually whether an item has been previously dunked by the host or not. In another series of experiments, grackles presented with pre-soaked items sometimes walked to the puddle before swallowing the items without dunking, suggesting that the distinction between dry and soaked items was not made visually upon collection of the food, but later while the food was held in the bill (Lefebvre unpubl. obs.). Other bird species have been found to target preferentially items of higher energetic value when value could be easily assessed by the kleptoparasites (food type or item size; Brockmann & Barnard 1979).

Many proto- or true tool use behaviours require releasing food items from the bill or hand during processing (e.g. food-dropping, use of a wedge or of a hammer). In Carib grackles, loss of physical control on food was an important determinant of kleptoparasitic attacks and successes. Grackles handling dry food sometimes deposit it on the ground or on a perch, but they usually hold it between the toes after doing so (Morand-Ferron, pers. obs.). Dunking grackles most often let food items fall into water from a standing position and then lowered the head to retrieve it (release technique). Despite being very brief, this period of loss of control on food seemed to render dunking grackles vulnerable to kleptoparasitism. A similar situation has been observed in Japanese macaques, where individuals throwing wheat grains on the surface of water were often kleptoparasitised by conspecifics, but not those holding potatoes in the hand and rubbing them free of sand in water (Kawai 1965). The release of items by hosts creates opportunities for stealthful kleptoparasitism, in which a thief can obtain an item while avoiding interaction with the host (Giraldeau & Caraco 2000). This strategy might allow successful kleptoparasitism by individuals who would usually lose in aggressive contests over food items. For example, subordinate ravens have been observed engaging in cache raiding (stealth kleptoparasitism), but not in aggressive displacement (Bugnyar & Kortschal 2002).

The rarity of the hold version of dunking behaviour in Carib grackles could be due to limited individual flexibility in the form of the behaviour exhibited. However, most dunking individuals (73.9 %) could use both techniques and some items were processed using a combination of the two techniques, which seems to rule out this possibility. An alternative explanation could be that the hold technique, despite reducing costs incurred through losses to food thieves, involves some other costs that the release technique does not confer. The increase in handling time associated with the use of the hold-while-dunking technique seems to support this explanation, but could also be due to other changes in the behaviour of birds dunking at high conspecific density (e.g. increased investment in conspecific monitoring, etc.). Other anti-kleptoparasitic behaviours have been shown to involve costs (Barnard & Stephens 1981; Schenkeveld & Ydenberg 1985; Vickery & Brooke 1994; Stienen & Brenninkmeijer 1999), thereby creating a trade-off between the risk of losing the item to kleptoparasites and the possible reduction in foraging rate through anti-theft action. Because they are often costly, protection behaviours must be performed flexibly, in accordance with variations in the risk of kleptoparasitism (Dally et al. 2006), which Carib grackles seemed to do by using the hold technique more often when conspecific density was high. Grackles also increased their use of aggressive head-up displays when subject to more kleptoparasitic attacks. This generally reduced food losses to kleptoparasites, but probably also involved costs in time, energy and risk of injury (mutual displays between a kleptoparasite and a potential host sometimes escalated into overt aggression; Morand-Ferron unpubl. obs.).

Overall, the probability of kleptoparasitic attempts and success on Carib grackles seemed to be more strongly determined by host behaviour than by characteristics of the host or of the item in its possession. Because of certain requirements of food processing behaviours, such as the need to release food items or to use a part of the environment where the density of competitors is high, food processing individuals might be particularly vulnerable to exploitation compared with individuals engaged in alternative foraging tactics. Comparative evidence suggests that tool and proto-tool use is more frequent in large-brained, innovative species (Lefebvre et al. 2002; Reader & Laland 2002). It is thus possible that, in such taxa, potential hosts are behaviourally flexible enough to avoid "scrounging costs" by resorting to alternative foraging tactics or engaging in anti-kleptoparasitic behaviours when foraging under high risk of food theft.

Acknowledgements

We would like to thank Donald L. Kramer, Simon M. Reader, Neeltje Boogert, Sarah E. Overington and two anonymous reviewers for helpful comments on a previous version of the paper. We are also grateful to Daniel Sol for his advice on statistical techniques. Funding for this work was provided by a Natural Sciences and Engineering Research Council of Canada (NSERC) grant to L.L. and a NSERC postgraduate scholarship to J.M.F. This study was conducted under McGill Animal Use Protocol number 4897 and complies with the laws of Barbados.

References

Barnard, C.J. & Stephens, H. 1981. Prey size selection by lapwings in lapwing/gull associations. Behaviour, 77, 1-22.

Beck, B.B. 1980. Animal tool behavior: the use and manufacture of tools by animals. New York: Garland.

Brockmann, H.J. & Barnard, C.J. 1979. Kleptoparasitism in birds. Animal Behaviour, 27, 487-514.

Bugnyar, T. & Kortschal, K. 2002. Scrounging tactics in free-ranging ravens, *Corvus corax*. Ethology, 108, 993-1009.

Burger, J. & Gochfeld, M. 1981. Age-related differences in piracy behaviour of four species of gulls. Behaviour, 77, 242-267.

Dally, J.M., Clayton, N.S. & Emery, N.J. 2006. The behaviour and evolution of cache protection and pilferage. Animal Behaviour, 72, 13-23.

Ens, B.J., Esselink, P. & Zwarts, L. 1990. Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*. Animal Behaviour, 39, 219-230.

Giraldeau, L.-A. & Caraco, T. 2000. Social foraging theory. Princeton: Princeton University Press.

Goodwin, D. 1986. Crows of the world, 2nd edn. London: British Museum.

Hickey, G. 2005. Dunking birds. Nature Australia, Winter, 16.

Jackson, J. 1985. The dunking habit of common grackles. American Birds, 39, 261-262.

Jaramillo, A. & Burke, P. 1999. New World blackbirds: the icterids. Princeton: Princeton University Press.

Johnson, K. & Peer, B.D. 2001. Great-tailed grackle. The Birds of North America, 576, 1-27.

Jones, C.G. 1979. Birds dunking food. British Birds, 72, 189-190.

Kawai, M. 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima islet. Primates, 6, 1-30.

Koenig, W.D. 1985. Dunking of prey by Brewer's blackbirds: a novel source of water for nestlings. Condor, 87, 444-445.

Kuss, O. 2002. How to use SAS for logistic regression with correlated data. SUGI, 27, 261.

Lefebvre, L., Nicolakakis, N. & Boire, D. 2002. Tools and brains in birds. Behaviour, 139, 939-973.

Morand-Ferron, J., Lefebvre, L., Reader, S.M., Sol, D. & Elvin, S. 2004. Dunking behaviour in Carib grackles. Animal Behaviour, 68, 1267-1274.

Norris, K., Freeman, A. & Vincent, J.F. 2000. The economics of getting high: decisions made by common gulls dropping cockles to open them. Behaviour, 137, 783-807.

Parker, S.T. & Gibson, K.R. 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. Journal of Human Evolution, 6, 623-641.

Post, W., Poston, J.P. & Bancroft, G.T. 1996. Boat-tailed grackle. The Birds of North America, 207, 1-19.

Reader, S.M. & Laland, K.N. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Science USA, 99, 4436-4441.

Schenkeveld, L.E. & Ydenberg, R.C. 1985. Synchronous diving by surf scoter flocks. Canadian Journal of Zoology, 63, 2516-2519.

Seibt, U. & Wickler, W. 1978. Marabou storks wash dung beetles. Zeitschrift fur Tierpsychologie, 46, 324-327.

Stevens, J.P. 2002. Applied multivariate statistics for the social sciences, 4th edn. Mahwah: Lawrence Erlbaum Associates.

Stienen, E.W.M. & Brenninkmeijer, A. 1999. Keep the chicks moving: how sandwich terns can minimize kleptoparasitism by black-headed gulls. Animal Behaviour, 57, 1135-1144.

Vickery, J.A. & Brooke, M. 1994. The kleptoparasitic interactions between great frigatebirds and masked boobies on Henderson island, South Pacific. Condor, 96, 331-340.

Visalberghi, E. & Fragaszy, D.M. 1990. Food-washing behaviour in tufted capuchin monkeys, *Cebus apella*, and crabeating macaques, *Macaca fascicularis*. Animal Behaviour, 40, 829-836.

Weekley, D.R. 1997. Eurasian sparrowhawk drowning Eurasian jay. British Birds, 90, 524-526.

Wiley, R.H. 1975. Multidimensional variation in an avian display: implications for social communication. Science, 190, 482-483.

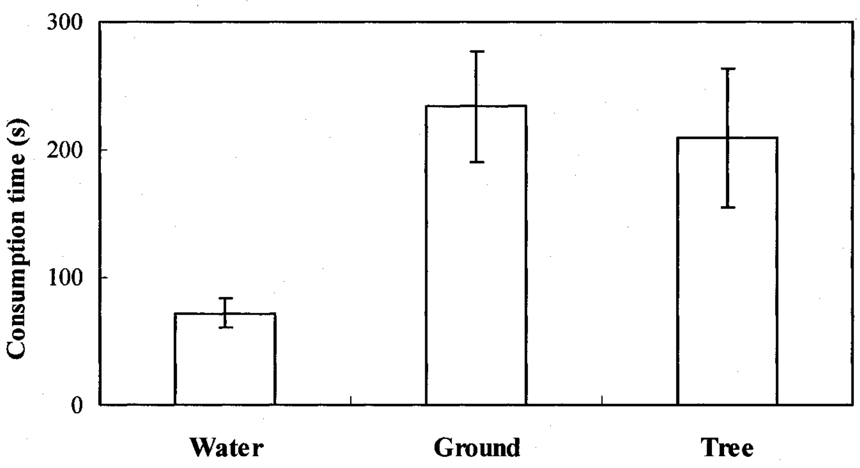

Fig. 5. Consumption time (mean ± standard error) when dunking (water; $n = 35$), depositing a dry item on the ground (ground; $n = 29$) or on a perch (tree; $n = 10$).

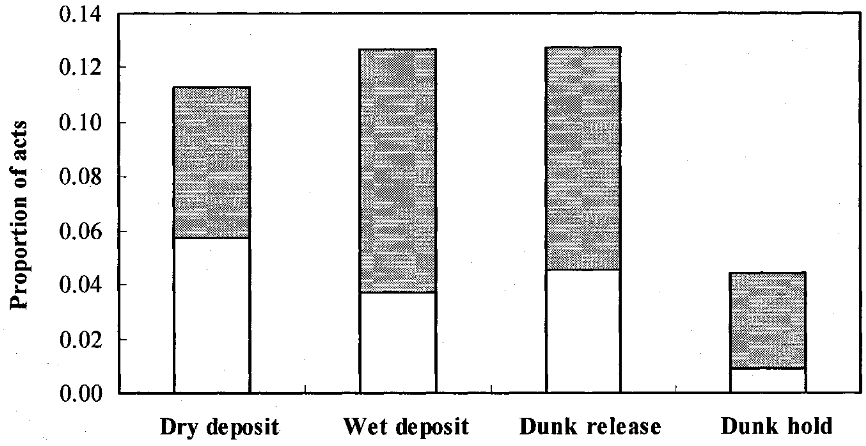

Fig. 6. Proportion of acts in which the focal bird lost its item to a kleptoparasite (in white) and received a missed kleptoparasitic attempt (in grey) for each type of behaviour recorded: deposit a dry item on the ground (dry deposit; *n* = 470), deposit a dunked item on the ground (wet deposit; *n* = 1030), dunk an item using the release technique (*n* = 2104), and dunk while holding an item in the bill (*n* = 545).

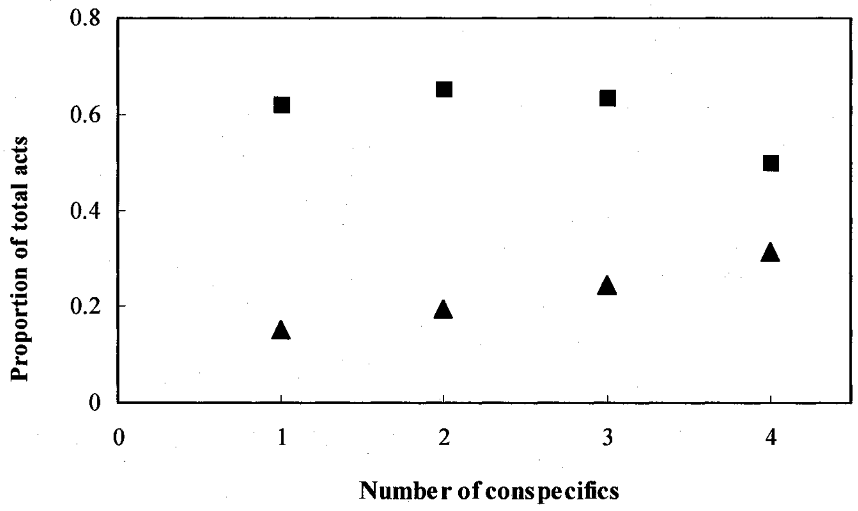

Fig. 7. Proportion of total acts performed at the study site that are dunk release (squares) and dunk hold (triangles) as a function of the number of conspecifics located 15 cm or less from the focal bird.

In Chapter 2, I studied determinants of kleptoparasitic host selection in Carib grackles and found that the behaviour of the potential host seemed to be a better predictor of its probability of being stolen from than its individual characteristics (no evidence of an effect of sex or age). Dunking seems to be a risky tactic because it involves manipulating food items at the water puddle, where the density of conspecific is high, and is most often performed by releasing items from the bill. Dunking birds avoided releasing items from the bill and performed more head-up displays when dunking under high risk of kleptoparasitism. The exact form of dunking behaviour, and the rate of expression of dunking versus alternative foraging tactics is not fixed, but depends on the prevailing conditions. This flexibility allowed examining the use of dunking and kleptoparasitism as two alternative tactics exhibited by grackles when feeding at our experimental food patches in the field. Here, I use the knowledge gained in the previous two chapters on the conditions influencing rates of dunking to devise field experiments looking at the effect of experimental manipulation of producing and scrounging costs on the frequency of both tactics. This study provides one of the first test of assumptions and predictions of producer-scrounger games in a wild animal.

Chapter 3.

Producing and scrounging in wild Carib grackles

Abstract

Producer-scrounger (PS) game-theoretical models make predictions about the decision of group-feeding animals either to look for food (produce) or for opportunities to exploit other foragers' discoveries (scrounge). In a PS game, the payoffs to scroungers are negatively frequency-dependent. We report the first empirical evidence of negative frequency-dependence of scroungers' payoffs obtained in the field, using observations on free-ranging Carib grackles (*Quiscalus lugubris*). As predicted by PS game models, experimental manipulations increasing the cost of using the scrounging tactic led to a decrease in the proportion of scroungers, and conversely, an increase in producing costs increased the proportion of scroungers in the group. We also found that increased producing costs were associated with a reduction in the size of flocks of free-ranging grackles, while experimental manipulations affecting the cost of using the scrounging tactic did not significantly influence group size. Observations on marked birds revealed that changes witnessed at the level of the whole group could be brought about at least partly by individual flexibility in tactic use. While most birds used both tactics and could alter their use of producing and scrounging when conditions changed, we also find consistent individual differences in tactic use.

Introduction

Group-feeding animals can either search for food themselves or exploit the foraging efforts of others by stealing (kleptoparasitism; Brockmann & Barnard, 1979) or joining discovered food patches (Giraldeau & Caraco 2000). This use of other's food discoveries can be analysed as an evolutionary game. Animals looking for their own food may be seen as producers and those exploiting the producers' foraging efforts may be seen as scroungers (Barnard & Sibly 1981). In producer-scrounger (PS) games, the payoffs obtained by scroungers depend on the proportion of the population engaged in each type of foraging behaviour: when scroungers are rare, they do better than when they are common, because they must then compete with a larger proportion of the population for a smaller number of scrounging opportunities. Barnard & Sibly (1981) applied the game to food joining within flocks of house sparrows but initially found only mixed support for the assumption: house sparrows (*Passer domesticus*) playing scrounger did better when there was at least one producer present in the flock, but did badly when there were several producers. Up to now, support for this assumption in a group foraging animal has come only from laboratory studies using captive flocks of nutmeg mannikins (*Lonchura punctulata*; Giraldeau et al., 1994; Mottley & Giraldeau 2000). In this paper, we provide the first confirmation of negative frequency-dependence of scrounger payoffs in a free-ranging animal.

The organism we used in our test is the Carib grackle (*Quiscalus lugubris*) of Barbados. *Q. lugubris* is a generalist passerine that feeds in groups on clumped food resources (mostly anthropogenic) in urban areas of Barbados (Jaramillo & Burke 1999). Grackles occasionally engage in dunking behaviour, the immersion of food items in water puddles before consumption (Morand-Ferron et al. 2004). This behaviour seems to ease the ingestion of hard and/or dry items, as evidenced by shorter handling times when eating dunked versus non dunked items (Morand-Ferron et al. 2006). Grackles have been observed to kleptoparasitise dunking individuals (Morand-Ferron et al. 2004; 2006). We ask whether the PS game can be used to analyse this kleptoparasitic behaviour where birds dunking food play producer, making more profitable food items available to scroungers.

PS game models predict that environmental changes altering the costs and benefits of producing and/or scrounging should cause group-feeding animals to converge on a new stable equilibrium, with changes increasing scrounging costs causing a decline in the proportion of scroungers in the group, and changes increasing producing costs having the opposite effect (Caraco & Giraldeau 1991). Evidence supporting this prediction has been gathered using captive flocks of nutmeg mannikins (*Lonchura punctulata*; Giraldeau et al. 1994; Mottley & Giraldeau 2000; Coolen et al. 2001; Barrette & Giraldeau 2006). Field studies on ravens (*Corvus corax*; Bugnyar & Kotrschal 2002b) and tree sparrows (*Passer montanus*; Liker & Barta 2002) have shown an increased use of the scrounging tactics at foraging patches associated with a greater risk of predation, and thus a higher cost of production. As a second goal of this paper, we provide the first experimental manipulation of both producing and scrounging costs in the field.

To manipulate producing cost, we altered travel time for dunking individuals. In the high producing cost condition, birds playing producer had to detour around a fence that was installed between the food pile and the water source at our experimental site. In the low producing cost condition, we created an opening in the fence, allowing birds to go directly and more quickly from the food pile to the water puddle when dunking food. To vary scrounging costs, we changed the perimeter-to-area ratio of the water puddle by changing its shape while keeping its surface area constant. In the low scrounging cost condition, the puddle had a round shape, and thus, a low perimeter-to-area ratio, while in the high scrounging cost condition, the puddle had an elongated, rectangular shape. Increasing the perimeter-to-area ratio of the puddle presumably allows birds to keep greater inter-individual distances, which should result in a lower probability of success for kleptoparasites (larger interindividual distances decrease losses to scroungers; Vines 1980; Ens & Goss-Custard 1984; Di Bitetti & Janson 2001). We tested whether flocks of wild grackles could adjust their use of producing and scrounging in the direction predicted by PS games: fewer producers when travel cost to the water was high and fewer scroungers when the shape of the puddle increased inter-individual distances.

Environmental conditions favouring an increase in the proportion of scroungers in foraging groups are thought to lead to lower average payoffs to all group members; i.e. scroungers impose a cost to group foraging (Vickery et al. 1991). If grackles indeed adjust their use of producing and scrounging to prevailing conditions in the field, our experimental site would be expected to be of lower value when producing costs are high and scrounging costs are low, because the proportion of scroungers is predicted to be higher then. One possible consequence of this is that grackles might reduce their use of this site in favour of other foraging sites, leading to a reduction in the size of flocks feeding at our experimental food patch. Because our test is done in the field, we can address this possibility for the first time, as tests on captive birds usually constrain their ability to leave the experimental situation. Foraging groups of wild Carib grackles can disperse and form quickly (Morand-Ferron, pers. obs.), leading to variable group size and composition over time and space. As a third goal of this paper, we examined whether the size of foraging groups of grackles would be smaller in the low scrounging cost condition that in the high scrounging cost condition, and larger in the low versus high producing cost condition.

Rapid group adjustment to variation in local foraging conditions is thought to result from individual flexibility in tactic use (Barnard & Sibly 1981; Caraco & Giraldeau 1991; Giraldeau & Caraco 2000). Previous work on grackles suggests that they show the individual flexibility required for the predicted adjustment (Morand-Ferron et al. 2004). In captivity, almost all grackles were capable of dunking when provided with dry food near water (31 of 36 of individually-caged wild-caught birds). Out of the 47 banded birds that engaged in dunking or stealing dunked food, twenty-six actually used both tactics. We would thus expect individual grackles to use dunking and stealing depending on the frequency-dependent costs and benefits of producing and scrounging. As the fourth goal of this paper, we tested this flexibility by monitoring marked birds in the field.

General material & methods

Field Observations

We observed Carib grackles foraging on a single food patch of indivisible items. In this system, the food patch is visible, so producers do not have to search for food, but they manipulate it through dunking behaviour and scroungers kleptoparasitize whole items during the dunking process. Field observations were conducted on a paved terrace located in the grounds of the Bellairs Research Institute of McGill University, in St. James, Barbados. At the beginning of each trial, the observer (JMF) placed ca. 200 dry dog food pellets (0.7 cm in diameter, 21 % protein, Atlantic Marketing, Barbados) in a clump on the ground 30 cm away from a round puddle of water ($A = 2000\ cm^2$, 2 cm deep). For Carib grackles, pellets are apparently difficult to swallow and to break. The food pile and puddle were replenished when they were approximately half-depleted and trials ended after 60 min, with a maximum of four trials per day (total = 85 trials). The experimenter observed from a distance of ca. 15 m and video recorded all trials. Between January 2002 and May 2004, 278 wild Carib grackles were caught, identified with unique colour band combinations, and released on the grounds of the Bellairs Institute. Sightings of banded birds were narrated into the camera microphone in order to insure correct identification of colour combinations upon data collection from the video recordings.

Experimental manipulations

In order to vary the cost of scrounging, we offered food and water in a low scrounging cost condition where the puddle was round (diameter = 50 cm; $A = 1964\ cm^2$), and in a high scrounging cost condition in which the puddle had the same surface area but had an elongated, rectangular shape (100 cm x 20 cm; $A = 2000\ cm^2$). In order to avoid order effects, we recorded data for five consecutive days in the low scrounging cost followed by five consecutive days in the high scrounging cost condition, and again five more consecutive days in the low scrounging cost condition. We then pooled both sets of observations conducted in the low cost condition.

In the low producing cost condition, the birds could walk directly from the food pile to the puddle (distance = 30 cm) through an opening in a wire mesh fence (1.5 m high x 4 m large) that had been placed on the site 5 days prior to testing. In the high producing cost condition, the opening was shut, forcing the birds to fly over or walk around the barrier. As the wire mesh fence was present in both conditions, differences between the treatments should not be due to eventual neophobic reactions to the fence. Birds were offered food and water for five successive days in the low producing cost condition. We then allowed one day for birds to habituate to the barrier while the opening was shut, ran five successive observation days in the high producing cost condition, and again five consecutive days in the low producing cost condition. All observations taken in the low cost condition were pooled together for analysis.

A. Negative frequency-dependence of scrounger payoffs

A major assumption of PS games is that scroungers should do better when they are rare than were they are common in the group. We thus predict a negative relationship between the payoffs obtained by scroungers and their proportion in groups of wild grackles.

Methods

We scanned videorecordings looking for kleptoparasitic attempts leading to successful stealing of a dunked item and consumption of this item by the scrounger. We noted the identity of the scrounger if the bird was banded, or its sex (Jaramillo & Burke 1999) when not marked. We calculated the time elapsed between the last feeding event or landing of the bird on the site and a successful kleptoparasitic event (latency to scrounge). Both types of observations were combined, as there was no effect of the behaviour of birds at the beginning of the foraging bout (landing or swallowing a previous item) on the latency to scrounge

($F_{1,23} = 0.02$, $p = 0.88$). To obtain a representation of the relative frequency of scroungers prevailing during this time, we noted the number of birds playing producer and scrounger at the water puddle at the time of landing or swallowing the last food item, and repeated this observation every 10 sec until the bird successfully stole the dunked item (including a count at this moment). We defined producers as birds who dunked and scroungers as birds (excluding the focal scrounger) who either made successful or unsuccessful theft attempts or waited at the water puddle. We calculated (1) group size by adding up the number of producers and scroungers at the puddle and (2) the proportion of birds that were playing scrounger at the puddle for each of these readings. We then averaged all readings taken during a same foraging bout by a focal scrounger.

The payoff to a focal scrounger was defined as the inverse of its latency to scrounge. As these payoffs are likely to vary with experimental conditions, and that, here, we are interested in variation within conditions only, we used data taken from a randomly chosen condition (second series of low scrounging cost condition). In order to ensure that the results could be generalised, we repeated the analysis on the first series of observations in the low producing cost condition, and obtained similar results (not shown). Because some data points were taken on birds that were not identified with colour bands (25 out of 41), we could not determine the number of independent data points in our sample. Moreover, data points taken within a same trial have a higher probability of being influenced by similar conditions (weather, time of day, etc.). To deal with these difficulties, we used generalised linear mixed-models for autocorrelated data. We modelled the variation in log-transformed payoffs to scroungers using the %GLIMMIX macro in SAS version 8.2 (Kuss 2001). We included the proportion of scroungers and group size as fixed factors, and individual and trial as random factors. The identity of unmarked birds was coded in two ways: once assuming that all unmarked individuals were different individuals, and once considering all unmarked females as one individual, and all unmarked males as one individual. We obtained similar results with both analyses, and will present only the latter as this coding system assumes more pseudoreplication than was probably the case and is thus more conservative.

Results

As predicted, the payoffs to scroungers declined as their proportion increased in the group ($F_{1,23} = 9.28, p = 0.006$; fig. 8). This effect held when controlling statistically for variation in group size ($F_{1,22} = 8.83, p = 0.007$).

B. Varying producing and scrounging costs

Here we examine the effect of experimental manipulations affecting the cost of using the scrounging and producing tactic on (1) the relative frequency of scroungers and (2) the size of foraging flocks of free-ranging grackles. We predict groups to be composed of a lower proportion of scroungers and a larger number of individuals in the high versus low scrounging cost condition, and in the low versus high producing cost condition.

Methods

We first need to verify that the experimental manipulations had the expected effect on scrounging and producing costs. In order to examine whether an increase in the perimeter-to-area ratio of the water puddle indeed led to an increase in scrounging costs, we noted the total number of successful and unsuccessful kleptoparasitic attempts occurring between the 15th and 30th minute of each trial. This is the period of observation that corresponded to maximal activity at the water puddle. We compared the proportion of successful attempts between the two conditions using a t-test.

The second type of manipulation involved opening or closing a large door in a wire fence placed between the food pile and the water puddle at our experimental site. We noted the time elapsed from the moment a grackle took an item from the pile until its arrival at the water puddle (travel time; data are taken between the 15th and 30th minute of each trial, excluding all cases where birds landed somewhere else before landing at the puddle). We compared log-transformed travel time between the two conditions using a t-test.

To test our predictions, we noted the number of birds playing producer and scrounger (defined in the same way as in the preceding section) every 10 sec using videorecordings. We calculated the proportion of scroungers and group size at the water puddle for each reading. We excluded all observations where there were either zero or only one bird at the puddle. We then averaged all readings in order to obtain only one data point per group size and proportion of scroungers for each trial. Because the proportion of scroungers has been shown to increase with the size of foraging groups (Coolen 2002; Barta et al. 2004), we used ANCOVAs with group size as a covariate to examine the effect of experimental manipulations on the proportion of scroungers in groups of grackles (both variables log-transformed). We compared mean group size (log-transformed) between conditions using a t-test.

Results

Verifying the effect of experimental manipulations

On average, grackles had to engage in more numerous kleptoparasitic attempts to successfully scrounge a dunked item in the high scrounging cost condition than in the low cost condition (0.48 ± 0.13 versus 0.37 ± 0.09 attempts/success, respectively; Two-sample t-test: $t = 3.2$, d.f. = 35, $p = 0.003$). In the second series of experiments, grackles transported a food item to water more quickly in the low versus high producing cost condition (2.39 ± 1.29 s versus 6.60 ± 1.18 s, respectively; Two-sample t-test: $t = -12.3$, d.f. = 30, $p < 0.001$).

Proportion of scroungers in the group

As predicted, the proportion of scroungers was lower when the cost of scrounging was high than when it was low ($F_{1,43} = 9.3$, $p = 0.004$; fig. 9a), and when the cost of producing was low versus high ($F_{1,36} = 43.4$, $p < 0.001$; fig. 9b). In these ANCOVAs, group size was positively correlated with the proportion of scroungers in the group while controlling for experimental condition (varying scrounging costs: $F_{1,43} = 15.7, p < 0.001$; varying producing costs: $F_{1,36} = 35.5, p < 0.001$).

Size of foraging flocks

Mean group size was higher in the low than in the high producing cost condition ($t = 3.61$, d.f. = 37, $p = 0.001$) but was not significantly different in the high versus low scrounging cost condition ($t = -1.33$, d.f. = 44, $p = 0.191$).

C. Individual flexibility in tactic use

Here, we use observations on marked birds to determine whether changes in the relative frequency of producers and scroungers between the different experimental conditions could have been brought about by individual flexibility in tactic use. We also ask whether individuals showed significant individual differences in tactic use, and whether these individual differences were consistent across experimental conditions.

Methods

We included in the analyses only marked individuals that were seen at least twice (60 marked birds observed, range = 1 to 393 acts per individual) in each of the conditions we compared. We defined the individual proportion of scrounging acts as the number of kleptoparasitic attempts (missed and successful) over the total number of acts (unsuccessful and successful kleptoparasitic attempts plus the number of items dunked, whether these were stolen by conspecifics or successfully eaten). In order to examine individual flexibility in tactic use, we ran a repeated-measures ANOVA on the arcsine square root transformed proportion of scrounging acts per condition for each individual (test of within-subjects effects). We analysed only the first set of data (varying scrounging costs; $n = 25$), as power for the second set was very low ($n = 8$, power = 0.075 with $\alpha = 0.05$). Individual differences were assessed with the between-subject effects test.

In order to examine individual consistency in tactic use, we ranked individuals observed to engage both in producing and scrounging according to their individual proportion of scrounging acts, and conducted a Wilcoxon signed ranks test. We also report the correlation between the proportion of scrounging acts by individuals observed in the low and high scrounging costs conditions.

Results

Most birds (22/25 individuals) used both the producing and scrounging tactics, while three birds engaged only in producing. We observed no pure scroungers.

Individual flexibility

When the cost of scrounging was experimentally increased, 15 individuals out of 25 (60 %) decreased their use of the scrounging tactic relative to producing, while seven birds did the opposite (28 %) and three birds were pure producers in both conditions (fig. 10). The alpha-probability for an overall decrease in the individual proportion of scrounging acts between the two conditions fell just short of the traditional threshold for significance ($F_{1,24} = 4.05$, $p = 0.056$). A test of between-subjects effects revealed significant individual differences in the proportion of scrounging acts ($F_{1,24} = 38.5$, $p < 0.001$).

Individual consistency

There were no significant differences in the ranking of individuals according to their proportion of scrounging acts between the low and high scrounging cost condition ($Z = -1.25$, $n = 22$, $p = 0.211$). The within-individual correlation in the proportion of scrounging acts between the two conditions was quite high (Pearson's correlation coefficient: $r = 0.843$; Bartlett $\chi^2 = 24.2$, d. f. = 1, $p < 0.001$).

Discussion

Our results provide the first evidence for the applicability of the PS game to a kleptoparasitic system in the field. We showed that for wild Carib grackles of Barbados (1) payoffs to scroungers were negatively frequency-dependent, (2) an increase in producing costs was associated with a reduction in foraging group size, while manipulations affecting scrounging costs did not significantly alter the size of flocks, (3) groups of grackles could adjust their use of the producing and scrounging tactics in response to experimental manipulation affecting producing and scrounging costs, and (4) individual birds exhibited some degree of flexibility and some degree of consistency in tactic use.

The payoffs obtained by individuals engaged in the scrounging tactic decreased when the relative frequency of scroungers increased in the group. This observation provides the first evidence for the assumption of negative frequency-dependence of payoffs to scroungers in a wild animal. This assumption constitutes one of the basic tenets of PS games, and has been previously confirmed only in captive nutmeg mannikins (Giraldeau et al. 1994; Mottley & Giraldeau 2000).

In the first test of a PS model, Barnard & Sibly (1981) suggested that captive individuals obtaining low payoffs in the current experimental conditions could choose to quit the group and stop foraging instead of foraging at a low rate. In the wild, animals have the additional option of travelling to another food patch when the value of the current option decreases below that of the average from the environment (Charnov 1976; Stephens & Krebs 1986). It follows that local conditions calling for a high frequency of scroungers at this food patch, and thus a low average rate of return for foragers (Vickery et al. 1991), might result in a reduction of the relative value of this patch and the departure of foragers towards other feeding sites. This is what seems to have occurred when we increased producing costs at our experimental site: the proportion of scroungers increased and group size decreased. We are unsure at this point why we did not observe the converse effect when scrounging costs were manipulated; one possibility is that the evaluation of patch quality could be linked more closely to costs and benefits of producing than scrounging, but this hypothesis remains to be tested. PS models usually assume that the size of the group is determined by other factors than the frequency of producers and scroungers (Giraldeau & Caraco 2000). Our results suggest that changes in conditions affecting the equilibrium frequency of producers and scroungers at a food patch might also act on the number of foragers attracted to the patch, and underline the importance of testing PS games in the field. Many taxa show moderate to high rates of change in feeding group composition (e.g. pigeons; Lefebvre & Giraldeau 1984), while fixed groups such as those formed in laboratory experiments probably correspond more closely to natural groups that have a cohesive structure (e.g. hyenas, Kruuk 1972; parids in winter, Desrochers 1989)

Wild groups of foraging grackles adjusted their use of producing and scrounging in the direction predicted by PS games following experimental manipulations of the costs of the tactics. Previous studies on free-ranging animals have used variation in predation risk as a way to vary the cost of producing (Bugnyar & Kotrschal 2002b; Barta et al. 2004). In our study, costs of using the producing tactic were manipulated by increasing the expense of time and energy birds had to invest when producing items (see also Giraldeau et al. 1994; Barrette & Giraldeau 2006). We also found that an increase in scrounging costs led to a decrease in the proportion of scroungers in groups of wild grackles. This result complements those obtained in captivity by Coolen et al. (2001) and Giraldeau & Livoreil (1998), who observed a reduction in the use of the scrounger tactic when the finder's share (amount of food that can be exploited exclusively by the producing individual) was increased. The observation that group-feeding animals show adjustment in tactic use to different means of manipulating producing and scrounging costs suggests that a variety of environmental variables may mediate the observed rates of producing and stealing in the wild (but see Robinette & Ha 2001).

Rapid group-level adjustments in the relative frequency of producers and scroungers have been suggested to result from individual flexibility in production and scrounging effort (Barnard & Sibly 1981; Caraco & Giraldeau 1991;

Giraldeau & Caraco 2000). We found some evidence for individual flexibility in tactic use, with most birds decreasing their use of scrounging when scrounging costs were increased. The effect across all birds almost reached significance, but a few individuals went in the opposite direction to that predicted. This mixed pattern is not unexpected in a frequency-dependent system. If many individuals decrease their use of a tactic when its environmental cost is increased, the frequency-dependent effects of the decrease might actually make an increase in the alternative tactic profitable for a few birds. Responses to experimental manipulations will thus be less homogenous than in situations where individuals behave independently of others and are expected to all change their behaviour in the same direction.

Although most grackles engaged in both producing and stealing behaviour, there was consistent variation in the proportional use of scrounging by different individuals, such that, on average, birds that engaged in a lot of producing in the high scrounging costs conditions were still producing at relatively high rates in the low scrounging cost condition. In previous field observations, we already noted that, although many birds both dunked and stole items from conspecifics in the field, the variation in dunking and kleptoparasitic rates was greater between than within individuals (Morand-Ferron et al. 2004). The presence of both consistency and flexibility in the response of animals exhibiting significant individual differences in tactic use (see Beauchamp 2001 for a similar result on zebra finches) is reminiscent of discussions on animal personalities (Sih et al. 2004; Dingemanse & Reale 2005). There have been many descriptions of limitations on the use of the producing or scrounging tactic (e.g. dominance, age, body size; Steele & Hockey 1995; Liker & Barta 2002; Bicca-Marques & Garber 2005). We do not know whether such constraints could explain individual differences in tactic use in wild Carib grackles. In previous work, however, the probability of engaging in dunking behaviour and to be robbed of food by conspecifics could not be explained by sex or age differences (Morand-Ferron et al. 2004; 2006). Between extreme cases where all individuals seem to be about equally inclined to use both tactics (e.g. nutmeg mannikins, starlings; Giraldeau et al. 1994; Koops & Giraldeau 1996), and cases where the use of producing and scrounging is determined phenotypically, a large number of taxa may exhibit some intermediate level of flexibility in tactic use.

Group-level adjustment in the relative frequency of scroungers could be achieved by other means than behavioural plasticity in cases where there are individual differences in tactic use and individuals have the possibility to leave and join foraging groups. One such possibility consists in phenotypic assortment of individuals to prevailing frequencies of producers and scroungers in different groups. Rita et al. (1997) have suggested that individuals that tend to produce should try to assort themselves with other producers in order to avoid the cost of foraging with scroungers. However, scroungers can be expected to join these groups, as they would then receive very high payoffs by foraging in a flock composed of a large proportion of producers. Because the payoffs to scroungers are negatively frequency-dependent, we might expect scroungers to leave groups where the frequency of scroungers exceeds the equilibrium, and to stay longer when feeding in or joining groups where the frequency of scroungers is below the equilibrium, thereby bringing back the group towards the stable equilibrium point. This would be consistent with Barnard & Sibly's (1981) prediction that the composition of groups that are at equilibrium should change less rapidly than those that are away from the equilibrium. This possible mechanism is not mutually exclusive with individual flexibility in tactic use, and both might contribute to restoring equilibrium frequencies of producers and scroungers after changes in local foraging conditions. We do not know whether this happened in Carib grackles, but it would be an interesting possibility to investigate in future studies.

Finally, it is interesting to note that we observed a qualitative fit of our results with predictions from PS games despite the fact that our study system differs in some points from biological systems for which PS models have been proposed. In our system, producers handle food instead of searching for it, and scroungers steal whole items instead of joining divisible food patches. We hope that this study will encourage field researchers to apply the PS framework to a wide range of biological systems in the wild.

Acknowledgements

We would like to thank Mélisa Veillette for her help in the field. We are also grateful to Frédérique Dubois for helpful comments on a previous version of the paper. Funding for this work was provided by an NSERC postgraduate scholarship to J.M.F and an NSERC grant to L.L. The study was conducted under McGill University Animal Use Protocol #4897 and complies with the laws of Barbados.

References

Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers - A general model and its application to captive flocks of house sparrows. Animal Behaviour, 29, 543-550.

Barrette, M. & Giraldeau, L. A. 2006. Prey crypticity reduces the proportion of group members searching for food. Animal Behaviour, 71, 1183-1189.

Barta, Z., Liker, A. & Monus, F. 2004. The effects of predation risk on the use of social foraging tactics. Animal Behaviour, 67, 301-308.

Beauchamp, G. 2001. Consistency and flexibility in the scrounging behaviour of zebra finches. Canadian Journal of Zoology, 79, 540-544.

Bicca-Marques, J. C. & Garber, P. A. 2005. Use of social and ecological information in tamarin foraging decisions. International Journal of Primatology, 26, 1321-1344.

Brockmann, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. Animal Behaviour, 27, 487-514.

Bugnyar, T. & Kotrschal, K. 2002. Scrounging tactics in free-ranging ravens, *Corvus Corax*. Ethology, 108, 993-1009.

Caraco, T. & Giraldeau, L. A. 1991. Social foraging - Producing and scrounging in a stochastic environment. Journal of Theoretical Biology, 153, 559-583.

Charnov, E. L. 1976. Optimal foraging, marginal value theorem. Theoretical Population Biology, 9, 129-136.

Coolen, I. 2002. Increasing foraging group size increases scrounger use and reduces searching efficiency in nutmeg mannikins (*Lonchura punctulata*). Behavioral Ecology and Sociobiology, 52, 232-238.

Coolen, I., Giraldeau, L. A. & Lavoie, M. 2001. Head position as an indicator of producer and scrounger tactics in a ground-feeding bird. Animal Behaviour, 61, 895-903.

Desrochers, A. 1989. Sex, dominance, and microhabitat use in wintering black-capped chickadees - A field experiment. Ecology, 70, 636-645.

Di Bitetti, M. S. & Janson, C. H. 2001. Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. Animal Behaviour, 62, 47-56.

Dingemanse, N. J. & Reale, D. 2005. Natural selection and animal personality. Behaviour, 142, 1159-1184.

Ens, B. J. & Gosscustard, J. D. 1984. Interference among Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*, on the Exe Estuary. Journal of Animal Ecology, 53, 217-231.

Giraldeau, L.-A. & Caraco, T. 2000. Social foraging theory. Princeton: Princeton University Press.

Giraldeau, L.-A. & Livoreil, B. 1998. Game theory and social foraging. In: Game theory and animal behaviour, (Ed. by L. A. Dugatkin and H. K. Reeve), pp. 16-37. Oxford: Oxford University Press.

Giraldeau, L. A., Soos, C. & Beauchamp, G. 1994. A Test of the Producer-Scrounger Foraging Game in Captive Flocks of Spice Finches, Lonchura-Punctulata. Behavioral Ecology and Sociobiology, 34, 251-256.

Jaramillo, A. & Burke, P. 1999. New World blackbirds: the icterids. Princeton: Princeton University Press.

Koops, M. A. & Giraldeau, L. A. 1996. Producer-scrounger foraging games in starlings: a test of rate-maximizing and risk-sensitive models. Animal Behaviour, 51, 773-783.

Kuss, O. 2002. How to use SAS for logistic regression with correlated data. SUGI, 27, 261.

Lefebvre, L. & Giraldeau, L. A. 1984. Daily feeding site use of urban pigeons. Canadian Journal of Zoology, 62, 1425-1428.

Liker, A. & Barta, Z. 2002. The effects of dominance on social foraging tactic use in house sparrows. Behaviour, 139, 1061-1076.

Morand-Ferron, J., Lefebvre, L., Reader, S. M., Sol, D. & Elvin, S. 2004. Dunking behaviour in Carib grackles. Animal Behaviour, 68, 1267-1274.

Morand-Ferron, J., Veillette, M. & Lefebvre, L. 2006. Stealing of dunked food in Carib grackles (*Quiscalus lugubris*). Behavioural Processes, In press.

Mottley, K. & Giraldeau, L. A. 2000. Experimental evidence that group foragers can converge on predicted producer-scrounger equilibria. Animal Behaviour, 60, 341-350.

Rita, H., Ranta, E. & Peuhkuri, N. 1997. Group foraging, patch exploitation time and the finder's advantage. Behavioral Ecology and Sociobiology, 40, 35-39.

Robinette, R. L. & Ha, J. C. 2001. Social and ecological factors influencing vigilance by Northwestern crows, *Corvus Caurinus*. Animal Behaviour, 62, 447-452.

Sih, A., Bell, A. M., Johnson, J. C. & Ziemba, R. E. 2004. Behavioral syndromes: an integrative overview. Quarterly Review of Biology, 79, 241-277.

Steele, W. K. & Hockey, P. A. R. 1995. Factors influencing rate and success of intraspecific kleptoparasitism among kelp gulls (*Larus dominicanus*). Auk, 112, 847-859.

Vickery, W. L., Giraldeau, L. A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991. Producers, scroungers, and group foraging. American Naturalist, 137, 847-863.

Vines, G. 1980. Spatial consequences of aggressive behavior in flocks of oystercatchers, *Haematopus ostralegus* L. Animal Behaviour, 28, 1175-1183.

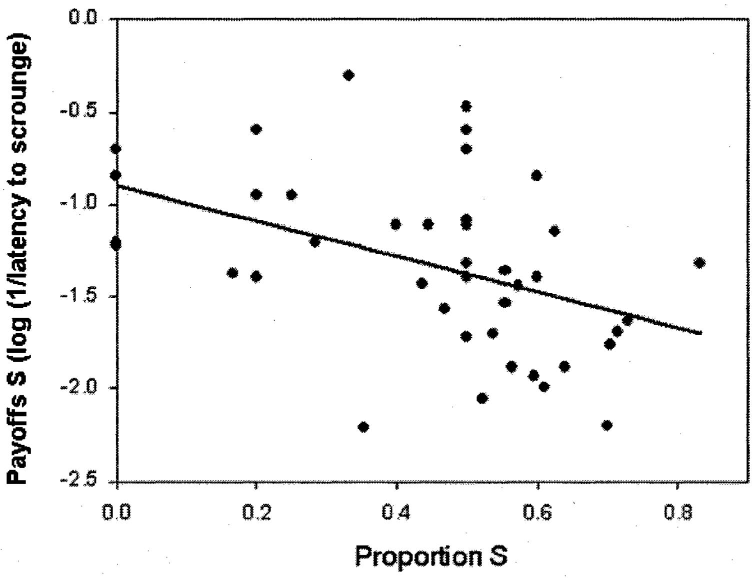

Figure 8. Payoffs to scroungers (log-transformed inverse of the latency to scrounge) as a function of the proportion of scroungers in the group.

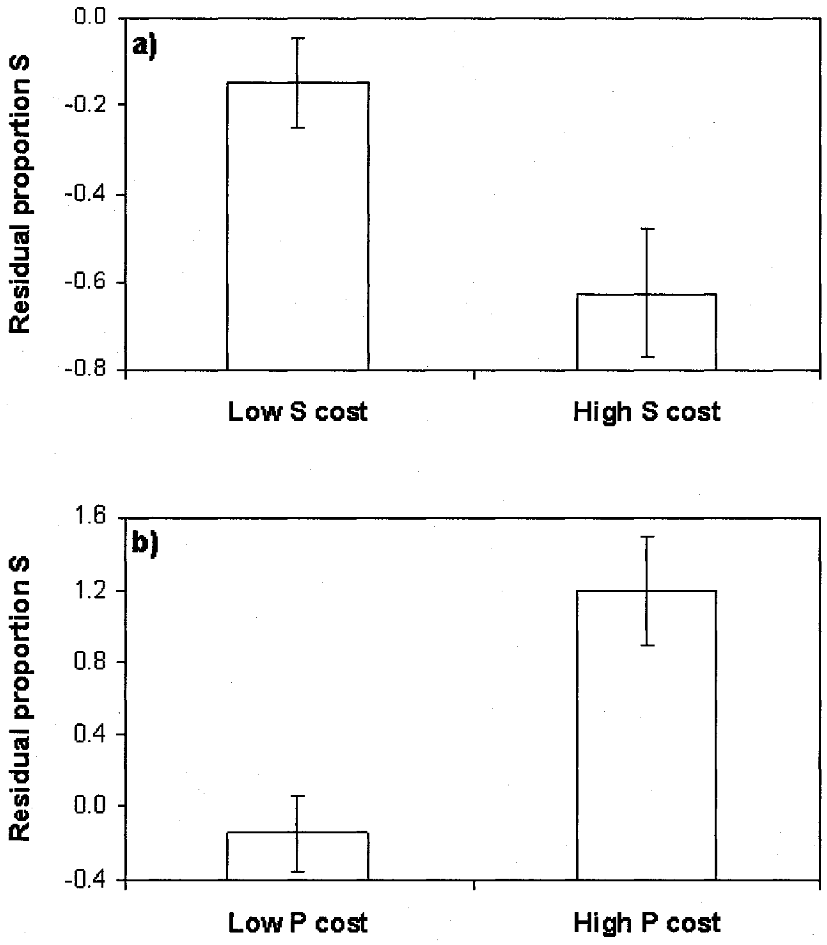

Figure 9. Mean (± standard error) residual proportion of scroungers (a) in the low versus high scrounging cost condition, and (b) in the low versus high producing cost condition. The residuals are obtained from a log-log regression of the proportion of scroungers against group size (all data pooled).

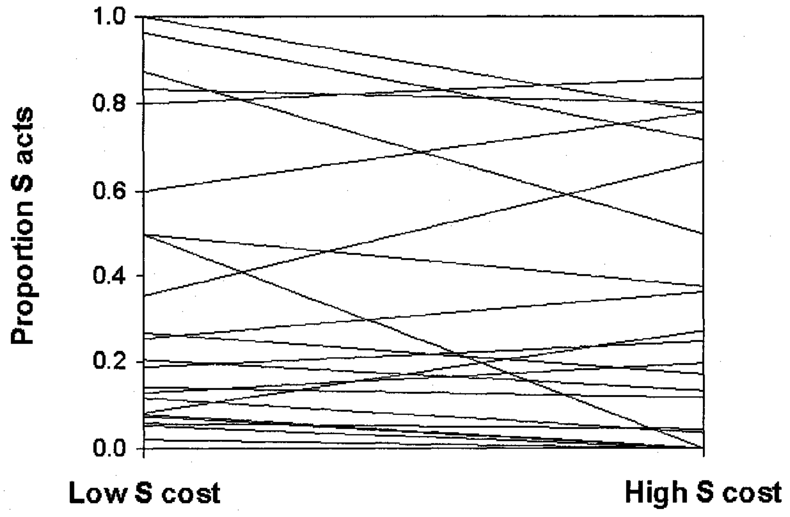

Figure 10. Proportion of scrounging acts by marked individuals ($n = 25$) in the low and high scrounging cost condition.

In the first two chapters, we found that intraspecific kleptoparasitism constituted an important cost to dunking behaviour, and examined how and why dunking birds were more vulnerable to food theft than non-dunking birds. We also looked at the behavioural response of grackles to variations in the risk of kleptoparasitism, and described two anti-kleptoparasitic behaviours performed by grackles. In Chapter 3, we examined the use of dunking and stealing of dunked food as alternative foraging tactics using a game-theoretical approach. Up to here, we thus looked at kleptoparasitism as a cost to intelligent behaviours that can depress their rate of expression in the wild by reducing their net payoffs and by constituting an alternative foraging tactic. In this last chapter, we ask the question as to whether kleptoparasitic behaviour itself might represent a form of intelligent behaviour: does the possession of a large brain favour the evolution of exploitative foraging tactics? Through an extensive literature search, we document the occurrence of kleptoparasitism in bird families and test several hypotheses on the ecological, morphological and behavioural predictors of food-stealing in birds. Here, we change our focus from intra- to interspecific kleptoparasitism for reasons of statistical power ($n = 152$ intraspecific cases versus 856 interspecific reports). However, as suggested by Brockmann & Barnard (1979), the two phenomenons might represent very similar behaviour. The observation that the taxonomic distribution of intra- and interspecific cases are not significantly different (Two-sample Kolmogorov-Smirnov, $D = 0.078$, $p = 0.8$; Morand-Ferron, unpubl. data) seems to argue in favour of this hypothesis.

Chapter 4.

Food-stealing in birds: brain or brawn?

Abstract

Kleptoparasitism, the stealing of food items already procured by others, is a widespread foraging strategy in animals. Despite the considerable interest that kleptoparasitism has attracted in recent times, the reasons why certain taxa have evolved such a strategy remain poorly understood. Here, using comparative information from 856 field reports of interspecific kleptoparasitism from all over the world, we test the different hypotheses that have been proposed for the evolution of food-stealing in birds. In multivariate analyses controlling for common ancestry effects, the probability that a family uses kleptoparasitism was positively associated with residual size of the brain and with the presence of vertebrate prey in the diet, but showed no association with body size, innovation rate or environmental variables like openness of the habitat or participation in mixed-species foraging groups. The relationship between brain size and kleptoparasitism was not due to potentially confounding variables such as mode of juvenile development or the degree of foliation of the cerebellum. The conclusion that kleptoparasitism is associated more closely with cognition than to aggression is supported by the fact that kleptoparasites have a larger residual brain size than their respective hosts, while their body size is not significantly larger. By emphasizing the central role of cognitive abilities in avian kleptoparasitism, our results offer a novel perception of avian food-stealing, which in the past was primarily seen in terms of "brawn" rather than "brains".

Introduction

Kleptoparasitism, the stealing of food discovered and captured by other foragers, is a pervasive phenomenon that has evolved in a variety of animals, including marine invertebrates (Iyengar 2004), insects and spiders (Vollrath 1984), fish (Grimm & Klinge 1996), reptiles (Cooper & Perez-Mellado 2003), birds (Brockmann & Barnard 1979) and mammals (Kruuk 1972; Brown et al. 2004). Now widely recognized as an important strategy by which many animals obtain limited resources (Giraldeau & Caraco 2000), the role of kleptoparasitism began to be appreciated 25 years ago, when Brockmann & Barnard (1979) published the first comprehensive review on the ecology of food-stealing in birds. This seminal work not only drew attention to the phenomenon, but also set the groundwork for a growing literature on where, when and how animals use kleptoparasitic strategies in the wild (e.g. Gorman et al. 1998; Goss-Custard et al. 1998; Ruxton & Broom 1999; Shealer et al. 2005). Despite this progress, the reasons why certain taxa have evolved food stealing while others have not continue to be obscure, although numerous hypotheses have been proposed (see below). The large amount of information on kleptoparasitism assembled in the last decades, particularly in birds, coupled with recent developments in phylogeny-based methods, now allows us to address this issue within a comparative framework. Here, we test alternative hypotheses that have been suggested to explain the evolution of kleptoparasitism with a comparative analysis in birds, using a dataset of more than 800 field reports from all over the world.

The benefits and costs that determine the profitability of food stealing are likely to depend on intrinsic characteristics that facilitate or constrain kleptoparasitic behaviour. In the ornithological literature, two sets of intrinsic characteristics appear to be crucial in determining the net success of food stealing. First, food stealing is often described as a form of aggressive food competition where thieves may use threats or actual physical aggression to force the host to abandon its prey item (e.g. Corkhill 1973; Maxson & Bernstein 1982; Tershy & Breese 1990). According to this aggressive competition perspective, larger birds would be at an advantage over smaller ones (Kushlan 1978; Temeles 1990; Cummins 1995; Willson & Marston 2002). A larger kleptoparasite might increase the probability of hosts yielding their food items, while reducing the probability of the host aggressively defending its prey. Kleptoparasitism should thus be more profitable, and hence have evolved, in lineages characterized by a large body mass, an idea we term the "brawn" hypothesis.

The second set of skills that might be useful in kleptoparasitic interactions relates to the tactical component of the behaviour. For kleptoparasitism to be profitable, it requires skills to select the appropriate hosts (Bélisle & Giroux 1995; Chavez-Ramirez 1995; Shealer et al. 1997) and to launch an attack from a suitable angle (Dunn 1973; Taylor 1979) or distance (Thompson 1986), using appropriate timing (Hesp & Barnard 1989) and locomotion mode (Burger & Gochfeld 1979). Moreover, it also requires the ability to accurately predict the behaviour of other animals (Krebs & Dawkins 1984) so as to avoid being detected while launching an attack (e.g. Furness 1978; Ens et al. 1990; Spear & Ainley 1993), as well as to anticipate either evasive or aggressive responses and counteractions by the host (Maxson & Bernstein 1982; Amat & Soriguer 1984). Cognitive abilities allowing the integration and use of more information in decision-making might thus increase the probability of kleptoparasitic success. A widely held assumption is that the size of the brain relative to that of the body reflects cognitive abilities of animals (Jerison 1973; Mace et al. 1980). Indeed, the relative size of the brain or of parts of the brain (i.e. neocortex in mammals and pallial areas in birds) has been found to correlate with learning speed (Gossette 1968; Riddell & Corl 1977), group size and/or social complexity (Barton 1996; Burish et al. 2004; Shultz & Dunbar 2006), frugivory (Clutton-Brock & Harvey 1980), capture of mobile prey (Garamszegi et al. 2002), and tool use (Lefebvre et al. 2002; Reader & Laland 2002). We predict kleptoparasites to have larger brains than birds that do not rely on this strategy ("brain" hypothesis).

Large-brained animals thus seem able to solve more complex ecological and social tasks. The extent to which animals can deal successfully with fluctuations in environmental conditions or change their behaviour when the more commonly used solutions are unfruitful is also thought to be an important aspect of cognition (Wyles et al. 1983; Reader & Laland 2002). This type of behavioural flexibility might allow species that do not possess specific adaptations to a kleptoparasitic lifestyle to recognise and take advantage of food-stealing opportunities occurring in their environment. In fact, this might well apply to most avian kleptoparasites, as even "specialised" kleptoparasites (e.g. frigatebirds, skuas) obtain only a fraction of their food through theft, and only during certain periods of the year (Brockmann & Barnard 1979; Furness 1987). As a corollary of the "brain" hypothesis, we predict taxa including food stealing in their foraging repertoire to exhibit high rates of foraging innovations, a field-based measure of behavioural flexibility and cognition (see Reader & Laland 2003, Lefebvre et al. 2004 for reviews).

Besides competitive and cognitive skills, the type of prey selected by birds has also been proposed to explain why certain taxa have evolved kleptoparasitism while others have not. In their review, Brockmann & Barnard (1979) noted that almost all kleptoparasitic families were predators including vertebrate prey in their diet. Vertebrate prey are most often large items of high energetic value requiring long handling times, factors that all have been shown to increase the probability and/or profitability of kleptoparasitic attacks in the field. Birds including vertebrate prey in their diet might therefore encounter profitable kleptoparasitic opportunities more often than non-predatory birds, and hence we expect them to have evolved the strategy more frequently ("predator" hypothesis). Attacking a host might also bear some similarities to attacking prey, pre-adapting predators to food theft.

In addition to intrinsic attributes of species, some ecological conditions might favour the evolution of food stealing by increasing the probability of encountering, detecting and/or pursuing successful foragers. An ecological condition that might influence the evolution of kleptoparasitism is the social foraging environment of the species. Food stealing has often been reported in large multispecific aggregations of seabirds (Furness 1987). Group feeding might increase the probability of kleptoparasitism because many unsuccessful and successful foragers can then be found in close proximity to each other (Brockmann & Barnard 1979; Amat 1990). The possibility that food stealing is a consequence of the social environment, which we term the "group-foraging" hypothesis, may be evaluated by testing whether kleptoparasites tend to join heterospecific foraging groups.

Finally, different types of habitats might offer varying opportunities for kleptoparasitism to be a rewarding strategy. In general, one expects open habitats such as grassland and marine habitats to offer better visibility and hence increase the probability of detecting potential hosts compared with closed habitats such as forests, where hosts might more easily go unnoticed (Paulson 1985). Thus, because of differences in habitat use, bird taxa may encounter kleptoparasitic opportunities at different rates, an idea we term the "habitat openness" hypothesis.

Our goals in the present paper are four-fold. First, we extensively review the relevant literature looking for field reports of kleptoparasitic behaviour in birds; we then use this information to demonstrate that the incidence of food stealing is non-randomly distributed across avian families. Secondly, we study the evolutionary history of kleptoparasitism with phylogeny-based methods to assess when and how often the strategy has evolved. The major conclusion of this analysis is that kleptoparasitism is an evolutionarily labile trait that depends on factors other than past history. Consequently, we test the five alternative hypotheses that have been proposed to favour the expression of kleptoparasitism. We employ phylogeny-based techniques that allow us to model variation in the incidence of food stealing across lineages as a function of clade traits and environmental variables while accounting for similarity between species due to common ancestry. While it is impossible to unambiguously diagnose the direction of causality by using comparative analyses (Bennett & Owens 2002), we deal with this problem by asking whether early differentiation in clade traits among avian families has shaped the subsequent evolution of kleptoparasitic strategies within the families. Finally, because we find that kleptoparasitic strategies are expressed more often in large-brained birds, we examine the contribution of potential confounding variables of the relationship between kleptoparasitism and cognition (juvenile development mode, cerebellum foliation index) and conduct a last analysis at a different taxonomic level by asking whether kleptoparasitic species have a larger neural substrate than that of their respective hosts.

Methods

We defined kleptoparasitism as the stealing of already procured food items (Brockmann & Barnard 1979). We searched for papers on kleptoparasitism in four electronic indexes of scientific publications for the period 1969-2002 (Web of Science, Biosis Preview, Zoological Records and Cisti Source), using keywords such as kleptoparasitism, stealing, piracy, theft, etc. We added these reports to cases listed in Brockmann and Barnard's appendix 1 (1979). Only papers reporting successful kleptoparasitism cases in which two birds interacted directly were included in the database (the full sequence of appropriation of prey by the kleptoparasite had to be witnessed by the observer). This excludes unsuccessful kleptoparasitic attempts, delayed kleptoparasitism (e.g. pilfering of food caches), and kleptoparasitism between a bird and an animal of another taxonomic group. We then split the cases in inter- versus intraspecific food stealing; in this paper, we concentrate on interspecific reports ($n = 856$).

We first test the two null hypotheses that kleptoparasitism distribution across bird families is explained by (i) common ancestry and (ii) research effort. We compared the frequency of species within families reported to show food stealing behaviour with that expected from either the total number of species in the family or the research effort devoted to each taxon. For the former, we multiplied the total number of species per family with the average proportion of kleptoparasitic species in the class Aves, 2.0% (197 kleptoparasitic species on a total of 9672; Sibley & Monroe 1990). The frequency of kleptoparasitism expected according to research effort was calculated from the online version of *The Zoological Record*, using the total number of papers published between 1978 and 2004. Differences between the distribution of observed and expected frequencies were assessed with the two-sample Kolmogorov-Smirnov test.

The second issue we explored is the importance of evolutionary history in explaining current-day variation in occurrence of food stealing in bird families. We chose to work at the family level because the phylogeny at this level is well supported in birds (Sibley & Ahlquist 1990) and because major diversification in basic life history traits have taken place before or during the establishment of contemporary families (Bennett & Owens 2002). The evolutionary history of food stealing was investigated with two phylogeny-based methods. First, we used parsimony reconstructions (Harvey & Pagel 1991) to map major transitions in the evolution of kleptoparasitism at the family level. A family was considered to have evolved the strategy if it contained at least one species reported to use kleptoparasitism. Second, we estimated the phylogenetic inertia in the proportion of kleptoparasites per family (number of species reported to perform kleptoparasitism/total species in the family) using the spatial autocorrelation statistic Moran's *I* (Gittleman & Kot 1990). We estimated Moran's *I* based on the phylogenetic hypothesis proposed by Sibley & Ahlquist (1990), using the Analysis of Phylogenetics and Evolution (APE) package in R (Paradis et al. 2004).

Because the above analyses suggested that food stealing has often evolved within families (see results), our third goal was to investigate the factors that could explain why some families have evolved kleptoparasitism, whereas others have not. We tested the five hypotheses presented earlier by modelling variation in the incidence of food theft across avian lineages as a function of body size, residual brain size, innovation rate, diet type, social foraging behaviour and habitat use.

To test the effect of body size on the occurrence of kleptoparasitism, we gathered data on body mass for 7,288 species, mostly based on information provided in Dunning (1993) and del Hoyo et al. (1992-2005). Repeatability of our body size measures were very high ($r = 0.99$). We used the mean of log-transformed species values to obtain family averages.

Brain mass was available for 1,967 species (Mlíkovský 1989a, 1989b, 1989c, 1990; DeVoogd et al. 1993; Székely et al. 1996; Garamszegi et al. 2002;

Iwaniuk & Nelson 2002; Iwaniuk 2003). When information was available from different sources, we used mean values. To remove the allometric effect of body size on brain mass (Jerison 1985; Van Schaik & Deaner 2003), we calculated the residuals from a log-log linear regression of total brain mass against body mass on species-level values, and then averaged these residuals within family groups. Our conclusions are robust with respect to the method used to calculate mean residual brain size; we obtained very similar results when using residuals from family means of log-tranformed body and brain masses (not shown; Pagel & Harvey 1989). It has been argued elsewhere that the number of cortical neurons (Roth & Dicke 2005) or the relative size of the nidopallium and mesopallium (Emery 2006) might represent more accurate measures of cognitive abilities. Unfortunately, these measures are only available for a restricted number of species. However, residual brain size correlates closely ($r^2 = 0.95$) with residual number of neurons (Herculano-Houzel 2006), and 96 % of the variance in the residual size of the mesopallium can be predicted by the residual size of the brain (Nicolakakis et al. 2003). The relative size of the whole brain thus represents a useful proxy for cognitive abilities in birds.

Because motor skills are thought to play an important role in kleptoparasitic behaviour (Brockmann & Barnard 1979), we looked at the contribution of the cerebellum in explaining variation in kleptoparasitic behaviour among bird families. The degree of foliation of the cerebellum is thought to reflect differences in sophistication of motor behaviour in birds and mammals (Butler & Hodos 1996). We thus entered the cerebellum foliation index in a model including body mass (all variables log-transformed prior to analysis). The data used in this analysis were taken from Table 1 in Iwaniuk et al. (2006). We also examine the partial contribution of juvenile development mode (taken from Bennett & Owens 2002) in explaining variation in the occurrence of kleptoparasitism among bird families because it is a known confounding variable of avian brain size, altricial birds having larger brains as adults than precocial ones (Portmann 1947; Bennett & Harvey 1985).

We used reports of innovative foraging behaviours taken from short notes sections of ornithological journals from six geographical regions (see Lefebvre et al. 1997 for examples). This measure has been tested for the potential biasing effect of nine confounding variables (e.g. observation and reporting biases by ornithologists; see Lefebvre et al. 2004 for a review) and is considered to be a valid estimate of behavioural flexibility in the field (Seyfarth & Cheney 2002; Reader & Laland 2003; Marino 2005). The innovation database includes reports of ingestion of a novel food type or use of a novel foraging technique. Reports consisting in attempted or successful kleptoparasitism were removed from the database (n = 111 of 2,397 cases in 808 species). We then used the residuals from a log-log linear regression of innovation frequency against research effort in families with at least one innovation report as our measure of innovation rate (see also Sol et al. 2005).

Information on diet and habitat (n = 105 families,) was taken from Bennett and Owens (2002). For diet type, we lumped together "Lower vertebrates", "Higher vertebrates" and "Animals" as predatory diets and "Folivore", "Frugivore", "Nectar" and "Invertebrate prey" as non-predators. We coded "Scrub", "Tundra", "Grassland, "Marine", "Marsh", "Freshwater" and "Land" as open habitats and "Forest" and "Woodland" as closed habitats. Information on participation in mixed-species foraging groups (coded as whether the family does or does not regularly join heterospecific groups; n = 100) was taken from the "Handbook of the birds of the world" (del Hoyo et al. 1992-2004). We gathered supplemental information (n = 24 families for diet, 19 for habitat and 23 for group-foraging) available from descriptions of families in the "Firefly Encyclopedia of Birds" (Perrins 2003) after we ascertained that the different sources provided similar information (> 90 % agreement in both cases).

We modelled the occurrence of kleptoparasitism as a function of the above variables, using phylogenetically-informed generalised estimating equations (GEEs), as implemented in R using the APE package (Paradis et al. 2004). Traditional statistical techniques assume that all data points are independent from one another, which is often not true in comparative analyses; closely related taxa have a higher probability of sharing characteristics retained from a common ancestor than taxa that are phylogenetically more distant (Felsenstein 1985). GEE analyses control for common ancestry by incorporating the phylogenetic relatedness among taxa as a correlation matrix in the model. This method yields results that are very close to independent contrasts in terms of type 1 error rate and power (Paradis & Claude 2002). We did in fact obtain similar results with contrasts, but GEE is more appropriate in our case as it provides typical GLM flexibility in the specification of the distribution of the response variable (binomial, Poisson, etc.) and allows us to accommodate both continuous and categorical variables as predictors. In keeping with our objective of examining whether kleptoparasitism was more likely to have evolved within lineages sharing certain attributes or environmental conditions, we characterised each family by the presence or absence of food stealing species and modelled this response variable with a binomial error structure and a logit link. Our results were robust with respect to the inclusion or exclusion of families coded as kleptoparasitic on the basis of only one record ($n = 6$) and we thus present here only analyses using the full dataset.

We first examined the effect of each predictor individually, including the total number of species per family (log-transformed) as the main confound in each model. Because species richness is closely correlated with research effort (Pearson's correlation coefficient: $r = 0.70$), its inclusion in the models can be thought of as a control for both speciosity and reporting biases. Second, we used a stepwise procedure to identify a minimum adequate model from all predictors and then conducted a multivariate GEE analysis using significant ($p < 0.05$) predictors only.

Our final goal was to validate the patterns found at the family level using the finer taxonomic level of species. We conducted paired analyses in which each kleptoparasitic species was compared with its host in terms of brain residual and body size. As both birds were foraging at the same location and were interested in the same food item at the moment of their observation in the field, this finer scale of analysis allows us to better control for ecological factors when explaining why one bird ended up winning the interaction while the other bird lost its prey to the kleptoparasite. We compared the kleptoparasite's and the host's relative brain size and body mass (log-transformed) using paired t-tests. In cases where a kleptoparasite was reported to steal from more than one host species, we averaged residual brain and body size values for the different hosts in order to include each kleptoparasite only once in the analysis. Because in some species body size may differ between sexes, we used sex-specific body mass when this information was available from the report, and species averages when it was not.

Results

Our review of the ornithological literature yielded 856 reports of interspecific kleptoparasitism by 197 species from 33 avian families (Fig. 11). The frequency of kleptoparasitic species could not be explained by speciosity (Kolmogorov-Smirnov: D = 0.77, $n = 143$, $p < 0.001$; fig. 11) or by research effort devoted to the families (Kolmogorov-Smirnov: D = 0.71, $n = 112$, $p < 0.001$).

A parsimony reconstruction revealed that kleptoparasitism has evolved repeatedly in a variety of phyletically distant families (Fig. 12). Interestingly, avian families were more dissimilar in the proportion of kleptoparasitic species than would be expected by chance (Moran's I autocorrelation index ± sd: -0.0147 ± 0.0013, $p < 0.0001$), suggesting that the strategy generally evolved within this taxonomic level rather than earlier in the evolutionary history of birds. The conclusion that kleptoparasitism is a labile trait is further supported by the finding that within families that have evolved the strategy, only some species have been reported stealing food (not shown).

The taxonomic distribution of kleptoparasitism among bird families thus cannot be explained solely by differences in speciosity or by phylogenetic autocorrelation. We next asked whether families sharing certain attributes or living in specific environments have a higher predisposition to evolve kleptoparasitism than families that do not share these attributes or environmental conditions. Having controlled for common ancestry and speciosity, the probability of evolving kleptoparasitic strategies was found to be significantly higher in families characterised by predatory habits, enlarged brain residuals and larger body masses, while innovation rate fell just short of the traditional threshold for significance (Table 2). However, there was no evidence that habitat use or participation in mixed-species foraging groups were associated with kleptoparasitism (Table 2). A stepwise procedure on all predictors yielded a minimum adequate model including speciosity, residual brain size and predatory diet. A phylogenetically-informed GEE model including these three predictors indicated that kleptoparasitism was positively associated with the total number of species per family ($t_{68} = 5.35, p < 0.001$), residual brain size ($t_{68} = 3.31, p = 0.002$) and predatory diet ($t_{68} = 2.37, p = 0.021$).

In order to verify that the association between kleptoparasitism and residual brain size was not due to the potentially confounding effect of juvenile development mode, we included both variables in a multivariate phylogenetically-informed GEE analysis. Residual brain size remained significantly associated with kleptoparasitic behaviour ($t_{56} = 3.04, p = 0.004$) while controlling for total number of species ($t_{56} = 4.80, p < 0.001$) and juvenile development mode ($t_{56} = 0.06, p = 0.95$).

The importance of residual brain size in explaining variation in kleptoparasitic behaviour in bird families might be interpreted in terms of improved cognitive abilities and/or perception and motor skills in large-brained birds. In order to examine the latter possibility, we entered cerebellum foliation index in a phylogenetically-informed multivariate model controlling for speciosity and body mass. Using this restricted data set ($n = 37$ families), the cerebellum foliation index was not a significant predictor of kleptoparasitic behaviour in birds families ($t_{23} = -1.09, p = 0.29$).

Finally, we found further support for the finding that kleptoparasitism is associated with cognition rather than to aggression in a species-level analysis comparing differences in residual brain size and body mass between kleptoparasites and their host(s). Kleptoparasites had a larger residual brain size than their respective hosts (Paired *t*-test: $t_{138} = 2.13, p = 0.035$). However, thieves were not heavier than their hosts (Paired *t*-test: $t_{190} = 0.37, p = 0.709$).

Discussion

Kleptoparasitism is a widespread phenomenon in birds and has evolved several times in the evolutionary history of the class. The evolutionary lability of kleptoparasitism may in part come from its opportunistic nature; avian kleptoparasites are capable of obtaining food through a wide variety of feeding techniques in addition to food stealing (Brockmann & Barnard 1979). Thus, food stealing might be a form of flexible foraging that allows predators to survive periods of low food availability. Support for this conclusion comes from the fact that innovative food stealing is often reported in the context of food shortages (e.g. Miller & Tilson 1985; Oro 1996). Nevertheless, the predisposition to develop kleptoparasitic behaviours is non-randomly distributed across avian taxa, and appears to be associated with certain attributes of the taxa. In particular, the type of prey and the possession of a large brain appear to have played an important role in favouring the evolution of kleptoparasitic feeding strategies in birds.

In their classic review, Brockmann & Barnard (1979) already noted that almost all kleptoparasitic families were predators including vertebrate prey in their diet. Vertebrate prey have a high energy content, are highly mobile and difficult to locate and/or capture, making kleptoparasitic attempts on this type of items absolutely and relatively more profitable than on other prey types (vegetable matter and invertebrates). Moreover, it is possible that morphological and behavioural adaptations useful in hunting vertebrate prey increase the probability of detecting and successfully exploiting kleptoparasitic opportunities in predatory taxa. Indeed, locating, pursuing and catching a prey from a mobile host might bear some behavioural similarities with hunting mobile prey. In frigatebirds, morphological adaptations allowing great speed and manoeuvrability in flight (see Nelson 1975) may be useful both in surface snatching of fish and in aerial pursuit of hosts. An evolutionary pathway from predation to kleptoparasitism has been proposed for *Argyrodes* spiders, that might have evolved stealing of insects from their host's web following missed predation events on web-building spiders (Vollrath 1984).

Our results are also consistent with Barnard's (1984) suggestion that scroungers are often opportunistic foragers with good cognitive capacities. Kleptoparasites had a larger residual brain size than their respective hosts foraging in the same environmental conditions. We also found that kleptoparasitism has evolved more frequently within families with larger brains relative to their body size, even after taking into account the effects of speciosity, diet type and common ancestry. This effect was not confounded by juvenile development mode, a well-known predictor of residual brain size in birds (Portmann 1947; Bennett & Harvey 1985). The possession of a large brain is thought to confer higher information-processing abilities, but might also allow for improved perception and motor skills. Sophistication of motor behaviour is thought to be reflected in the degree of foliation of the avian cerebellum (Butler & Hodos 1996), which is itself correlated with the size of the cerebellum and of the whole brain (Iwaniuk et al. 2006). We found no evidence that cerebellum foliation index could predict variation in kleptoparasitic behaviour among the 37 families for which data were available. This does not mean that motor skills do not play a role in food-stealing, only that the cognitive abilities associated with a large brain are better predictors of kleptoparasitic behaviour than are more specific differences in cerebellar foliation. This conclusion is in any case tentative, as the taxonomic data set for cerebellar foliation is currently much smaller than that of whole brain size.

The precise role of cognition in successful interspecific kleptoparasitic acts has not been extensively studied yet, but some field studies suggest an effect of learning independent of physical maturation and/or social dominance. For example, immature black-headed gulls (*Larus ridibundus*) are less successful kleptoparasites than adults, despite no apparent differences in body dimensions and in the speed and strength of attacks (Hesp & Barnard 1989). Success of immatures increased as they engaged in fewer mistimed attacks, which often lead to detection of the attack and evasion by lapwings (*Vanellus vanellus*).

Large-brained birds are, on average, behaviourally more flexible than small-brained birds. For example, the propensity of feeding innovations in birds correlates positively with relative size of the whole brain and residual size of the forebrain and mesopallium (Lefebvre et al. 1997; Timmermans et al. 2000), a region involved in higher-order functions such as integration of information from different modalities (Reiner et al. 2005). Our results on the link between innovation rate and food stealing fell just short (0.064) of the traditional threshold for significance, making it difficult to conclude one way or the other on this measure of flexibility.

The important finding that kleptoparasitism is associated with brain size contrasts with the weak evidence supporting a similar role for contest competition skills. In univariate analyses, kleptoparasitism was positively associated with body mass at the family level, but this effect was lost in the multivariate analysis including other predictors. In the species-level paired analysis, thieves were not found to be significantly larger than the hosts they steal from. Similarly, in a review on kleptoparasitism in seabirds, Furness (1987) found 33 pairs of kleptoparasites where the victim was heavier than the host, and 21 with the opposite pattern, resulting in no significant differences in body mass between kleptoparasites and their hosts. Larger birds might be at an advantage in contexts where they can use threats or actual physical aggression on the host ("aggressive kleptoparasitism" in Giraldeau & Caraco 2000), but not necessarily in cases where the kleptoparasite surprises the host and leaves with the prey before the host can detect or react to the attack ("stealth kleptoparasitism" in Giraldeau & Caraco 2000). Furthermore, acceleration speed might be important in many kleptoparasitic pursuits, and a smaller body then provides a higher power output (Pennycuick 1975). These conflicting effects might explain the weak predictive power of body size in explaining the distribution of kleptoparasitism in birds. However, it is still possible that the use of family and species averages have masked the size differences that might exist between each individual kleptoparasite and its victim, despite our effort at minimising this possibility by using sex-specific body mass whenever possible in the paired analysis.

Environmental factors also had little predictive power in explaining variation between families in the evolution of kleptoparasitism. After controlling for speciosity and common ancestry, we found no effect of habitat openness and multispecific group foraging. In a paper on kleptoparasitism by predatory birds, Paulson (1985) noted that ten out of 22 species foraging primarily in open habitats have been reported to engage in food-stealing while none of the ten woodland species do so. However, this study did not control for the higher probability of observing an infrequent behaviour in open habitats. Without being a significant determinant of the presence or absence of kleptoparasitism in different taxa, these ecological conditions might still have an influence on actual rates of food-stealing in the wild, with kleptoparasitic species engaging in more frequent attacks and/or obtaining higher success when participating in mixed aggregations and foraging in open habitats. For example, some birds of prey and mammalian carnivores are thought to reduce kleptoparasitic losses by consuming prey in covered areas (Fischer 1985; Newton 1986; Packer 1986). Similarly, birds might increase their kleptoparasitic intake while feeding in multispecific aggregations, but interspecific sociality might not lead to innovative food-stealing in taxa that have low behavioural flexibility. In mixed-species foraging groups, larger-brained species usually rob smaller-brained species, despite the fact that both species feed simultaneously on the same food items in the same ecological conditions. For example, gulls (*Larus ridibundus*) rob earthworms from lapwings and golden plovers (*Pluvialis apricaria*; Thompson 1986), and drongos (*Dicrurus paradiseus*) steal insects from laughing thrushes (*Garrulax pectoralis*; King & Rappole 2001), but the reverse is not observed.

The finding that avian kleptoparasites may be depicted as large-brained predators not only confirms previous suggestions by Brockmann & Barnard (1979) and Barnard (1984), but also emphasizes the general importance of clade attributes in the evolution of kleptoparasitism. These results do not invalidate the case-by-case importance of other factors such as social dominance, type of habitat or social environment in determining kleptoparasitic success, but suggest that these factors are unlikely to be general explanations for understanding why certain taxa have evolved kleptoparasitism whereas others have not. A major implication of our conclusions is the need to give more attention to cognitive processes in the study of heterospecific kleptoparasitic strategies. To date, most studies looking at cognitive abilities related to food stealing and prevention of thievery have examined interactions within species rather than among species. These studies have revealed surprising flexibility in protection behaviours by potential hosts (e.g. food-caching corvids, reviewed in Dally et al. 2006) and kleptoparasitic tactics (e.g. ravens act inconspicuously while watching conspecifics caching food, Bugnyar & Kotrschal 2002; pigs follow and displace knowledgeable subordinates, Held et al. 2000; baboons use a conspecific in displacing a competitor from food, Byrne & Whiten 1985). Some avian taxa even appear capable of creating kleptoparasitic opportunities by giving false alarm calls and stealing items while flock mates are engaged in anti-predator vigilance (Munn 1986; Møller 1988). This type of behaviour allows stealing from conspecifics as well as heterospecifics, and might represent just one of the tactical behaviours performed by birds to usurp a desirable food resource. Deceptive acts by primates are often performed in food-related contexts, and are more frequent in species with a large neocortex (Byrne & Corp 2004), drawing an interesting parallel with our findings in birds.

Acknowledgements

We would like to thank Emmanuel Paradis, Ted Garland and Brian McGill for statistical advice, and two anonymous reviewers for valuable comments on a previous version of the manuscript. Funding for this work was provided by an NSERC grant to L.L. and an NSERC and FQRNT scholarships to J.M.F.

References

Amat, J. A. 1990. Food usurpation by waterfowl and waders. Wildfowl, 41, 107-116.

Amat, J. A. & Soriguer, R. C. 1984. Kleptoparasitism of coots by gadwalls. Ornis Scandinavica, 15, 188-194.

Barnard, C. J. 1984. The evolution of food-scrounging strategies within and between species. In: Producers and scroungers: strategies of exploitation and parasitism (Ed. by C. J. Barnard), pp. 95-126. New York: Chapman & Hall.

Barton, R. A. 1996. Neocortex size and behavioural ecology in primates. Proceedings of the Royal Society of London Series B-Biological Sciences, 263, 173-177.

Bélisle, M. & Giroux, J.-F. 1995. Predation and kleptoparasitism by migrating parasitic jaegers. Condor, 97, 771-781.

Bennett, P. M. & Harvey, P. H. 1985. Relative brain size and ecology in birds. Journal of Zoology (London), 207, 151-169.

Bennett, P. M. & Owens, I. P. F. 2002. Evolutionary ecology of birds. Oxford: Oxford University Press.

Brockmann, H. J. & Barnard, C. J. 1979. Kleptoparasitism in birds. Animal Behaviour, 27, 487-514.

Brown, G. R., Almond, R. E. A. & Van Bergen, Y. 2004. Begging, stealing, and offering: food transfer in nonhuman primates. Advances in the Study of Behaviour, 34, 265-295.

Bugnyar, T. & Kotrschal, K. 2002. Observational learning and the raiding of food caches in ravens: is it 'tactical' deception? Animal Behaviour, 64, 185-195. (DOI 10.1006/anbe.2002.3056)

Burger, J. & Gochfeld, M. 1979. Age differences in ring-billed gull kleptoparasitism on starlings. Auk, 96, 806-808.

Burish, M. J., Kueh, H. Y. & Wang, S. S.-H. 2004. Brain architecture and social complexity in modern and ancient birds. Brain Behavior and Evolution, 63, 107-124. (DOI 10.1159/000075674)

Butler, A. B. & Hodos, W. 1996. Comparative vertebrate neuroanatomy. New York: Wiley-Liss.

Byrne, R. W. & Corp, N. 2004. Neocortex size predicts deception rate in primates. Proceedings of the Royal Society of London Series B-Biological Sciences, 271, 1693-1699. (DOI 10.1098/rspb.2004.2780)

Byrne, R. W. & Whiten, A. 1985. Tactical deception of familiar individuals in baboons (*Papio ursinus*). Animal Behaviour, 33, 669-673.

Chavez-Ramirez, F. 1995. Sex-biased kleptoparasitism of hooded merganser by ring-billed gulls. Wilson Bulletin, 107, 379-382.

Clutton-Brock, T. H. & Harvey, P. H. 1980. Primates, brains and ecology. Journal of Zoology (London), 190, 309-323.

Cooper, W. E. Jr. & Pérez-Mellado, V. 2003. Kleptoparasitism in the Balearic lizard, *Podarcis lilfordi*. Amphibia-Reptilia, 24, 219-224.

Corkhill, P. 1973. Food and feeding ecology of puffins. Bird Study, 20, 207-220.

Cummins, R. E. 1995. Sex-biased host selection and success of kleptoparasitic behaviour of the great frigatebird in the Northwestern Hawaiian islands. Condor, 97, 811-814.

Dally, J. M., Clayton, N. S. & Emery, N. J. 2006. The behaviour and evolution of cache protection and pilferage. Animal Behaviour, 72, 13-23. (DOI 10.1016/j.anbehav.2005.08.020)

Del Hoyo, J. Elliott, A. & Sargatal, J. 1992. Handbook of the birds of the world, vol. 1. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Sargatal, J. 1994 Handbook of the birds of the world, vol. 2. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Sargatal, J. 1996. Handbook of the birds of the world, vol. 3. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Sargatal, J. 1997. Handbook of the birds of the world, vol. 4. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Sargatal, J. 1999. Handbook of the birds of the world, vol. 5. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Sargatal, J. 2001. Handbook of the birds of the world, vol. 6. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Sargatal, J. 2002. Handbook of the birds of the world, vol. 7. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Christie, D. 2003. Handbook of the birds of the world, vol. 8. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Christie, D. 2004. Handbook of the birds of the world, vol. 9. Barcelona: Lynx Edicions.

Del Hoyo, J. Elliott, A. & Christie, D. 2005. Handbook of the birds of the world, vol. 10. Barcelona: Lynx Edicions.

DeVoogd, T. J., Krebs, J. R., Healy, S. D. & Purvis, A. 1993. Relations between song repertoire size and the volume of brain nuclei related to song: comparative evolutionary analyses amongst oscine birds. Proceedings of the Royal Society of London Series B-Biological Sciences, 254, 75-82.

Dunn, E. K. 1973. Robbing behaviour of roseate terns. Auk, 90, 641-651.

Dunning, J. B. 1993. CRC handbook of avian body masses. Boca Raton: CRC Press.

Emery, N. J. 2006. Cognitive ornithology: the evolution of avian intelligence. Philosophical Transaction of the Royal Society Series B, 361, 23-43.

Ens, B. J., Esselink, P. & Zwarts, L. 1990. Kleptoparasitism as a problem of prey choice: a study on mudflat-feeding curlews, *Numenius arquata*. Animal Behaviour, 39, 219-230.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist, 125, 1-15.

Fischer, D. L. 1985. Piracy behaviour of wintering bald eagles. Condor, 87, 246-251.

Furness, R. W. 1978. Kleptoparasitism by great skuas (*Catharacta skua Brünn.*) and arctic skuas (*Stercorarius parasiticus L.*) at a Shetland seabird colony. Animal Behaviour, 26, 1167-1177.

Furness, R. W. 1987. Kleptoparasitism in seabirds. In: Seabirds: feeding ecology and role in marine ecosystems (Ed. by J. P. Croxall), pp. 77-100. Cambridge: Cambridge University Press.

Garamszegi, L. Z., Møller, A. P. & Erritzoe, J. 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. Proceedings of the Royal Society of London Series B-Biological Sciences, 269, 961-967. (DOI 10.1098/rspb.2002.1967)

Giraldeau, L.-A. & Caraco, T. 2000. Social foraging theory. Princeton: Princeton University Press.

Gittleman, J. L. & Kot, M. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. Systematic Zoology, 39, 227–241.

Gorman, M. L., Mills, M. G., Raath, J. P. & Speakman, J. R. 1998. High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaeanas. Nature, 391, 479-480.

Goss-Custard, J. D., Cayford, J. T. & Lea, S. G. 1998. The changing trade-off between food finding and food stealing in juvenile oystercatchers. Animal Behaviour, 55, 745-760.

Grimm, M. P. & Klinge, M. 1996. Pike and some aspects of its dependence on vegetation. In: Pike: biology and exploitation (Ed. by J. F. Craig), pp. 125-126. London: Chapman & Hall.

Harvey, P. H. & Pagel, M. D. 1991. The comparative method in evolutionary biology. Oxford: Oxford University Press.

Held, S., Mendl, M., Devereux, C. & Byrne, R. W. 2000. Social tactics of pigs in a competitive foraging task: the 'informed forager' paradigm. Animal Behaviour, 59, 569-576. (DOI 10.1006/anbe.1999.1322)

Herculano-Houzel, S. 2006. Encephalization correspond to neuronal excess in rodents. Nature, submitted.

Hesp, L. S. & Barnard, C. J. 1989. Gulls and plovers: age-related differences in kleptoparasitism among black-headed gulls (*Larus ridibundus*). Behavioral Ecology & Sociobiology, 24, 297-304.

Iwaniuk, A. N. 2003. The evolution of brain size and structure in birds. Ph.D. thesis, Monash University, Clayton, Victoria, Australia.

Iwaniuk, A. N., Hurd, P. L. & Nelson, J. E. 2006. Comparative morphology of the avian cerebellum: I. Degree of foliation. Brain Behavior and Evolution, 68, 45-62.

Iwaniuk, A. N. & Nelson, J. E. 2002. Can endocranial volume be used as an estimate of brain size in birds? Canadian Journal of Zoology, 80, 16-23. (DOI 10.1139/Z01-204)

Iyengar, E. V. 2004. Host-specific performance and host use in the kleptoparasitic marine snail *Trichotropis cancellata*. Oecologia, 138, 628-639. (DOI 10.1007/s00442-003-1467-1)

Jerison, H. J. 1973. Evolution of the brain and intelligence. New York: Academic Press.

Jerison, H. J. 1985. Animal intelligence as encephalization. Philosophical Transactions of the Royal Society Series B, 308, 21-35.

King, D. I. & Rappole, J. H. 2001. Mixed-species bird flocks in dipterocarp forest of north-central Burma (Myanmar). Ibis, 143, 380-390.

Krebs, J. R. & Dawkins, R. 1984. Animal signals: mind-reading and manipulation. In: Behavioural ecology: an evolutionary approach, 2nd ed (Ed. by J. R. Krebs & N. B. Davies), pp. 380-402. Sunderland: Sinauer Associates.

Kruuk, H. 1972. The spotted hyaena: a study of predation and social behaviour. Chicago: University of Chicago Press.

Kushlan, J. A. 1978. Nonrigorous foraging by robbing egrets. Ecology, 59, 649-653.

Lefebvre, L., Nicolakakis, N. & Boire, D. 2002. Tools and brains in birds. Behaviour, 139, 939-973.

Lefebvre, L., Reader, S. M. & Sol, D. 2004. Brains, innovations and evolution in birds and primates. Brain Behavior and Evolution, 63, 233-246. (DOI 10.1159/000076784)

Lefebvre, L., Whittle, P., Lascaris, E. & Finkelstein, A. 1997. Feeding innovations and forebrain size in birds. Animal Behaviour, 53, 549-560.

Mace, G. M., Harvey, P. H. & Clutton-Brock, T. H. 1980. Is brain size an ecological variable? Trends in Neuroscience, 3, 193-196.

Marino, L. 2005. Big brains do matter in new environments. Proceedings of the National Academy of Sciences of the United States of America, 102, 5305-5307. (DOI 10.1073/pnas.0501695102)

Maxson, S. J. & Bernstein, N. P. 1982. Kleptoparasitism by south polar skuas on blue-eyed shags in Antarctica. Wilson Bulletin, 94, 269-281.

Miller, B. W. & Tilson, R. L. 1985. Snail kite kleptoparasitism of limpkins. Auk, 102, 170-171.

Mlíkovský, J. 1989a. Brain size in birds: 1. Tinamiformes through Ciconiiformes. Vést. cs. Spolec. Zool. 53, 33-45.

Mlíkovský, J. 1989b. Brain size in birds: 2. Falconiformes through Gaviiformes. Vést. cs. Spolec. Zool. 53, 200-213.

Mlíkovský, J. 1989c. Brain size in birds: 3. Columbiformes through Piciformes. Vést. cs. Spolec. Zool. 53, 252-264.

Mlíkovský, J. 1990. Brain size in birds: 4. Passeriformes. Acta Soc. Zool. Bohemoslov. 54, 27-37.

Møller, A. P. 1988. False alarm calls as a means of resource usurpation in the great tit *Parus major*. Ethology, 79, 25-30.

Munn, C. A. 1986. Birds that cry wolf. Nature, 319, 143-144

Nelson, J. B. 1975. The breeding biology of frigatebirds - A comparative review. Living Bird, 14, 113-156.

Newton, I. 1986. The sparrowhawk. Calton: Poyser.

Nicolakakis, N. Sol, D. & Lefebvre, L. 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. Animal Behaviour, 65, 445-452.

Oro, D. 1996. Interspecific kleptoparasitism in Audouin's gull *Larus audouinii* at the Ebro Delta, northeast Spain: a behavioural response to low food availability. Ibis, 138, 218-221.

Packer, C. 1986. The ecology of sociality in felids. In: Ecological aspects of social evolution: birds and mammals (Ed. by D. I. Rubenstein & R. W. Wrangham), pp. 429-451, Princeton: Princeton University Press.

Pagel, M.D. & Harvey, P.H. 1989. Taxonomic differences in the scaling of brain on body weight among mammals. Science, 344, 1589-1593.

Paradis, E. & Claude, J. 2002. Analysis of comparative data using generalized estimating equations. Journal of Theoretical Biology, 218, 175-183. (DOI 10.1006/yjtbi.3066)

Paradis, E., Claude, J. & Strimmer, K. 2004. APE : analyses of phylogenetics and evolution in R langage. Bioinformatics, 20, 289-290. (DOI 10.1093/bioinformatics/btg412)

Paulson, D. R. 1985. The importance of open habitat to the occurrence of kleptoparasitism. Auk, 102, 637-639.

Pennycuick, C. J. 1975. Mechanics of flight. Avian Biology, 5, 1-75.

Perrins, C. 2003. Firefly encyclopedia of birds. Oxford: Andromeda.

Portmann, A. 1947. Étude sur la cérébralisation chez les oiseaux. II. Alauda 15, 1-15.

Reader, S. M. & Laland, K. N. 2002. Social intelligence, innovation, and enhanced brain size in primates. Proceedings of the National Academy of Sciences of the United States of America, 99, 4436-4441. (DOI 10.1073/pnas.062041299)

Reader, S. M., & K. N. Laland. 2003. Animal innovation. Oxford University Press, Oxford.

Reiner, A., Yamamoto, K. & Karten, H. J. 2005. Organization and evolution of the avian forebrain. Anatomical Record, 287A, 1080-1102. (DOI 10.1002/ar.a.20253)

Roth, G. & Dicke, U. 2005. Evolution of the brain and intelligence. Trends in Cognitive Sciences, 9, 250-257. (DOI 10.1016/j.tics.2005.03.005)

Ruxton, G. D. & Broom, M. 1999. Evolution of kleptoparasitism as a war of attrition. Journal of Evolutionary Biology, 12, 755-759.

Seyfarth, R. M. & Cheney, D. L. 2002. What are big brains for? Proceedings of the National Academy of Sciences of the United States of America, 99, 4141-4142. (DOI 10.1073/pnas.082105099)

Shealer, D. A., Floyd, T. & Burger, J. 1997. Host choice and success of gulls and terns kleptoparasitizing brown pelicans. Animal Behaviour, 53, 655-665.

Shealer, D. A., Spendelow, J. A., Hatfield, J. S. & Nisbet, I. C. T. 2005. The adaptive significance of stealing in a marine bird and its relationship to parental quality. Behavioral Ecology, 16, 371-376.

Shultz, S. & Dunbar, R. I. M. 2006. Both social and ecological factors predict ungulate brain size. Proceedings of the Royal Society of London Series B-Biological Sciences, 273, 207-215. (DOI 10.1098/rspb.2005.3283)

Sibley, C. G. & Ahlquist, J. E. 1990. Phylogeny and classification of birds. New Haven: Yale University Press.

Sibley, C. G. & Monroe, B. 1990. Distribution and taxonomy of birds of the world. New Haven: Yale University Press.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. Proceedings of the National Academy of Sciences of the United States of America, 102: 5460-5465. (DOI 10.1073/pnas.0408145102)

Spear, L. & Ainley, D. G. 1993. Kleptoparasitism by kermadec petrels, jaegers, and skuas in the Eastern tropical Pacific: evidence of mimicry by two species of Pterodroma. Auk, 110, 222-233.

Székely, T., Catchpole, C. K., DeVoogd, A., Marchl, Z. & DeVoogd, T. J. 1996. Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylvidae). Proceedings of the Royal Society of London Series B-Biological Sciences, 263, 607-610.

Taylor, I. R. 1979. The kleptoparasitic behaviour of the Arctic skua *Stercorarius parasiticus* with three species of tern. Ibis, 121, 274-282.

Temeles, E. J. 1990. Interspecific territoriality of northern harriers: the role of kleptoparasitism. Animal Behaviour, 40, 361-366.

Tershy, B. R. & Breese, D. 1990. The influence of sexual dimorphism on kleptoparasitism of blue-footed boobies by brown boobies. Canadian Journal of Zoology, 68, 197-199.

Thompson D. B. A. 1986. The economics of kleptoparasitism: optimal foraging, host and prey selection by gulls. Animal Behaviour, 34, 1189-1205.

Timmermans, S., Lefebvre, L., Boire, D. & Basu, P. 2000. Relative size of the hyperstriatum ventrale is the best predictor of feeding innovation rate in birds. Brain Behavior and Evolution, 56, 196-203. (DOI 10.1159/000047204)

Van Schaik, C. P. & Deaner, R. O. 2003. Life history and cognitive evolution in primates. In: Animal social complexity (Ed. by F. B. M. de Waal and P. L. Tyack), pp. 5-25. Cambridge: Harvard University Press.

Vollrath, F. 1984. Kleptobiotic interactions in invertebrates. In: Producers and scroungers: strategies of exploitation and parasitism (Ed. by C. J. Barnard), pp. 61-94. New York: Chapman & Hall.

Willson, M. F. & Marston, B. H. 2002. Fishing success of gulls at a southeast Alaska smelt run. Journal of Field Ornithology, 73, 91-96.

Wyles, J. S., Kunkel, J. G. & A. C. Wilson. 1983. Birds, behavior and anatomical evolution. Proceedings of the National Academy of Sciences of the United States of America, 80, 4394-4397.

Table 2. Predictors of interspecific kleptoparasitism in six phylogenetically-informed univariate GEE analyses. Each analysis included the total number of species per family (log-transformed) as the main confounding variable. The number of phylogenetic degrees of freedom is indicated under *dfP*.

Model	*N*	*Estimate*	*t*	*p*	*dfP*
1. Nb spp + Body mass	129	0.68	2.05	0.045	68.0
2. Nb spp + Residual brain size	129	0.84	3.51	<0.001	68.0
3. Nb spp + Innovation rate	74	0.57	1.91	0.064	39.3
4. Nb spp + Predatory diet	129	1.87	2.60	0.011	68.0
5. Nb spp + Multispecific groups	123	0.56	1.19	0.240	65.6
6. Nb spp + Open habitat	124	-0.21	-0.44	0.661	65.9

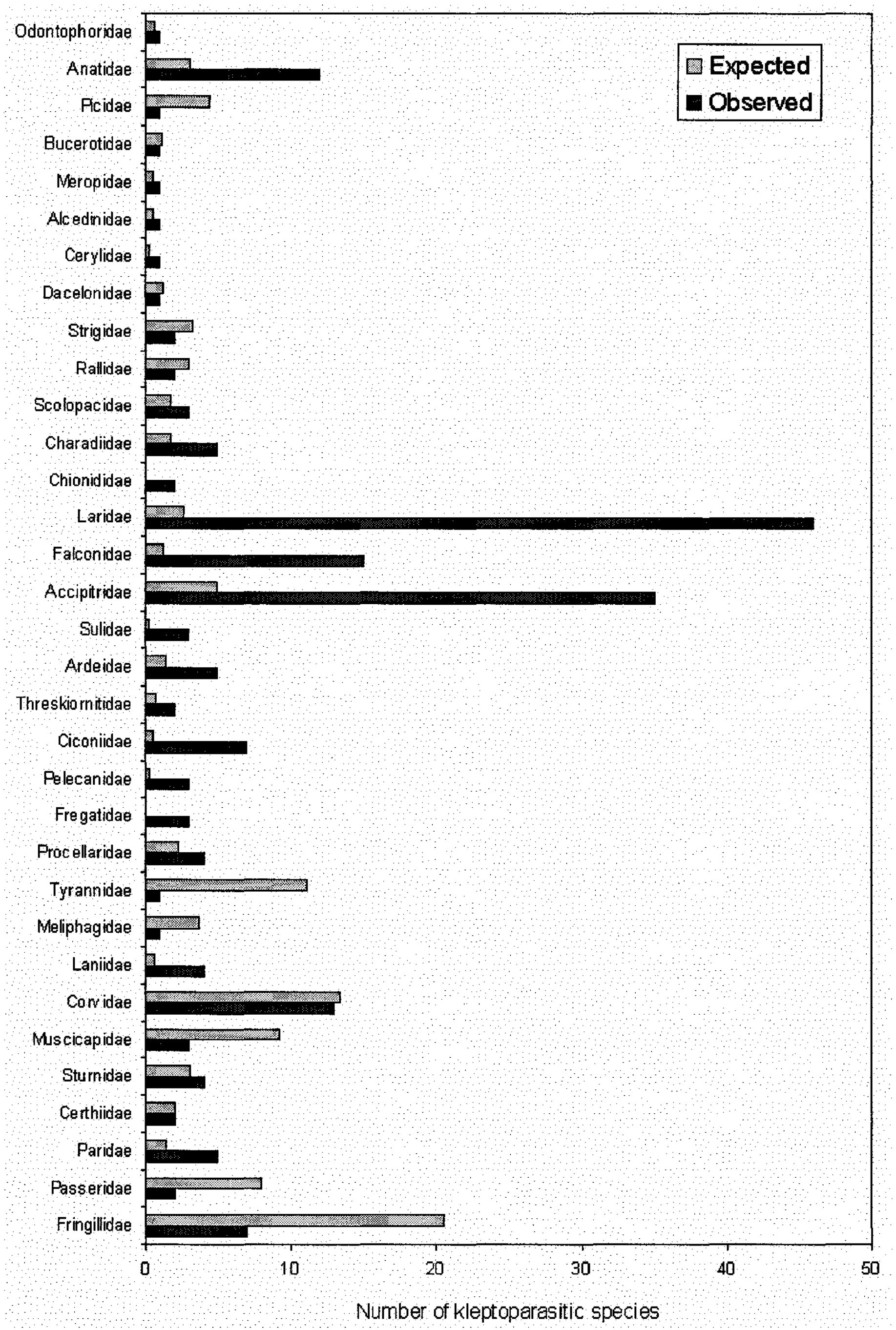
Odontophoridae
Anatidae
Picidae
Bucerotidae
Meropidae
Alcedinidae
Cerylidae
Dacelonidae
Strigidae
Rallidae
Scolopacidae
Charadiidae
Chionididae
Laridae
Falconidae
Accipitridae
Sulidae
Ardeidae
Threskiornitidae
Ciconiidae
Pelecanidae
Fregatidae
Procellaridae
Tyrannidae
Meliphagidae
Laniidae
Corvidae
Muscicapidae
Sturnidae
Certhiidae
Paridae
Passeridae
Fringillidae
▨ Expected
■ Observed
0
10
20
30
40
50
Number of kleptoparasitic species

Figure 11. Observed (in black) and expected (in grey) number of kleptoparasitic species in the 33 families where kleptoparasitism is present. Expected frequencies are calculated from the total number of species per family. The position of families on the graph reflects their genetic proximity in Sibley & Alquist (1990).

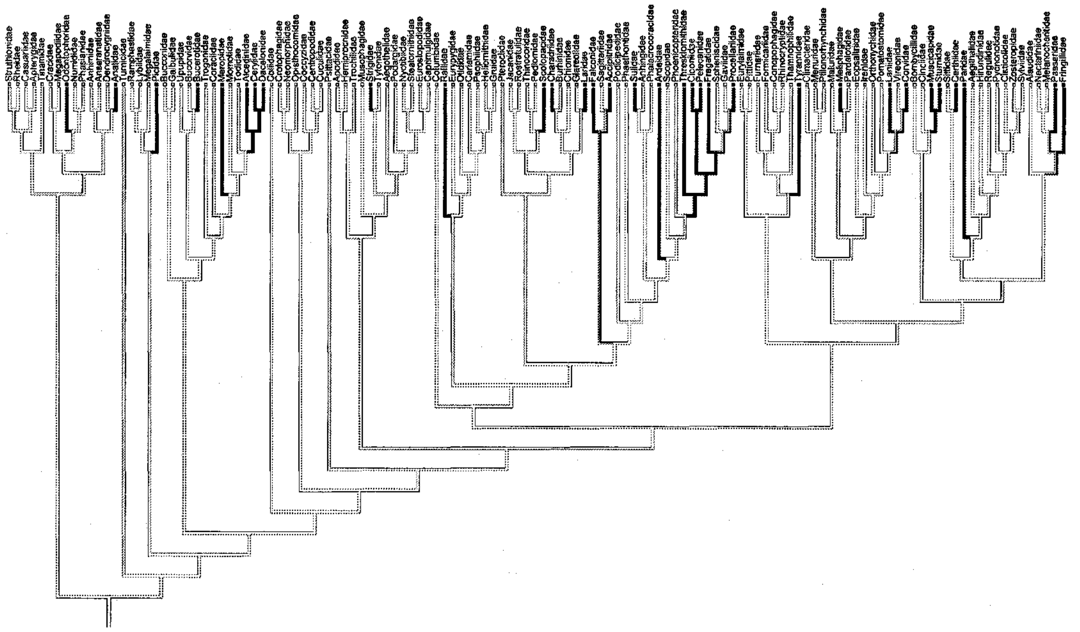

Figure 12. Evolution of kleptoparasitism in birds, based on the phylogenetic hypothesis proposed by Sibley & Ahlquist (1990). The evolution of kleptoparasitism, represented as solid bars, is estimated with parsimony ancestral state reconstruction.

General Conclusion

In the General Introduction, I briefly reviewed a set of operational definitions of intelligence in animals. Whether based on experimental tests or quantitative analyses of taxonomic distributions, all the definitions point to the relative rarity of animal intelligence. This rarity suggests that there are important costs that might balance the potential benefits of intelligence. The costs of evolving and maintaining a large brain constrain cognition in many taxa. However, even in cases where encephalisation is sufficient for intelligent behaviours to be possible, the frequency of expression of these behaviours is not fixed, but appears to depend on current costs and benefits. The observed frequency of intelligent behaviours thus does not always reflect the number of individuals who know how to perform them. For example, Tebbich and colleagues (2001; 2002) showed that juvenile woodpecker finches from dry and humid environments could learn to use twigs as tools to dislodge insects from tree bark. In the field, however, the frequency was high in the dry zone but very low in the humid zone. Similarly, although dunking rates are low in the field, almost all captive Carib grackles in my experiments could perform the behaviour in favourable conditions (Chapter 1). Moreover, dunking rates of individuals observed both in the field and in captivity were significantly different, suggesting that costs and benefits to the behaviour might vary in different contexts for different individuals. Rates of dunking in the field were not fixed, but depended on costs and benefits to dunking and food-stealing (Chapter 1 and 3).

One cost to innovative solutions and tool-use in the foraging context consists in the exploitation of the products of intelligent behaviours by conspecifics or heterospecifics through food-stealing. Kleptoparasitism is important in foraging because it can influence prey selection (Galef et al. 2001; Dekker 2003), vigilance (Goss-Custard et al. 1999; Robinette & Ha 2001), aggression and territoriality (Temeles 1990; McKechnie et al. 1994), interspecific associations (Stahler et al. 2002), group size (Cooper 1991; Hamilton & Dill 2003) and group productivity (Vickery et al. 1991). The perceived risk of kleptoparasitism might influence the rate of expression of foraging tactics that are particularly susceptible to theft. There are several reasons why tool and proto-tool users might be subject to particularly high rates of food-stealing: high relative value of food, large investment in searching and/or obtaining items, high learning costs, loss of physical control of food. Dunking in Carib grackles provides an ideal situation to compare stealing rates on items handled with and without proto-tool behaviour. In Chapter 1, I found that grackles dunking food were more often robbed than those taking similar items from the same food pile but not engaging in dunking behaviour. Dunking seemed to be a risky technique because it involved releasing items in water, a part of the environment where the density of conspecifics is high (Chapter 2). The exploitation costs of an innovative proto-tool use behaviour could thus be systematically studied.

Theft depressed rates of dunking in the field. In Chapter 1, I observed (1) a negative relationship between the density of conspecifics at the water puddle and the rate of dunking, and (2) a positive relationship between density and probability of kleptoparasitism. This situation is analogous to individuals "playing dumb" under a high risk of exploitation. In macaques, for example, subordinates do not perform foraging behaviours they know when dominants are present (Drea & Wallen 1999). Kleptoparasitism may thus contribute to the apparent low rates of expression of intelligent behaviours in the field through inhibition of their expression in favour of an alternative foraging tactic that is less susceptible to exploitation (i.e. flying away with dry food in grackles). Stealing by individuals that know how to dunk is not just a cost to dunkers, but also an alternative foraging tactic that further decreases dunking frequency (Barnard & Sibly 1981). In Carib grackles, many individuals engaged in both dunking and stealing dunked food in the field; some birds that could actually perform dunking were thus often looking for opportunities to steal dunked food. In Chapter 3, dunking frequencies were further reduced when costs to scrounging were lowered; 15 birds out of 25 then increased their use of scrounging relative to producing. In such a frequency-dependent system, the decision to engage in producing versus scrounging is influenced by physical conditions (e.g. travel costs to producing, proximity to potential scroungers), but also by the behaviour of group mates.

Learning was not studied in this thesis, as almost all birds examined in captivity spontaneously performed dunking. If this had not been the case, the obvious next step would have been to look at individual and social routes to the adoption of dunking behaviour. Many innovations might be "lost" because they represent exploratory behaviour leading to suboptimal payoffs (Reader & Laland 2003); in some cases scrounging and kleptoparasitism may further contribute to reducing these payoffs. Scrounging is known to block the learning of producing behaviours in pigeons (Giraldeau & Lefebvre 1987; Lefebvre & Helder 1997). In other cases, however, scrounging might actually facilitate the social learning of a task (Caldwell & Whiten 2003; Gajdon et al. 2006). For example, stealing parts of a nut cracked open by a conspecific capuchin monkey can contribute to developing nut-cracking skills (Ottoni et al. 2005).

In situations where intelligent behaviours provide high payoff, individuals might engage in strategies aimed at reducing losses to kleptoparasites by engaging in anti-kleptoparasitic behaviour. These behaviours might consist in modifying some aspects of the behaviour such that the vulnerability to food thieves is reduced, or engaging in protective behaviour such as aggressive defence of items. For example, birds decrease the height of food-dropping flights when surrounded by a larger number of conspecifics, thereby minimising the period during which they are vulnerable to kleptoparasitism (Whiteley et al. 1990; Cristol & Switzer 1999). Some group-living gulls have even been observed to aggressively defend a dropping site (Barash et al. 1975). Our field observations on Carib grackles also revealed the use of anti-kleptoparasitic tactics by dunking birds; grackles performed aggressive head-up displays when encountering kleptoparasitic attempts, and held items in the bill instead of releasing them in water when dunking under a high risk of theft (Chapter 2). Because anti-kleptoparasitic tactics are often costly, they must be performed flexibly, depending on variation in the risk of kleptoparasitism (Chapter 2; Dally et al. 2006). In contexts where kleptoparasitic costs are high, animals might be selected for the ability to evaluate the risk of kleptoparasitism and act to minimize it. Conversely, when benefits to food-stealing are high, food thieves might gain by finding a way to counter these anti-kleptoparasitic behaviours. When both behaviours may contribute to the survival of individuals (different individuals from the population might engage in each tactic or all individuals might resort to the two tactics), an arms race might ensue, selecting for the individuals with the best ability at defeating their opponents' move. This has been suggested to occur in food-caching corvids (Bugnyar & Kotrschal 2002a).

The use of kleptoparasitic strategies might thus consist in much more than a 'brawny' aggressive alternative to 'brainy' foraging tactics; kleptoparasites might themselves have to be endowed with considerable skills at predicting the behaviour of their hosts to be able to take advantage of it (Barnard 1984). This view of kleptoparasitism as a tactical behaviour has already been put forward by Barnard (1984) and Byrne & Whiten (1988). However, the general opinion on kleptoparasitism is often that it is "an easy meal", with larger, dominant, and/or more aggressive animals simply winning contests over weaker ones. In Chapter 4, I have tested these two views of kleptoparasitism in birds, and I showed that although there is a positive effect of a large body in univariate analyses, residual brain size seems to be a much more powerful predictor of the evolution of kleptoparasitism among bird families. Moreover, kleptoparasites had a larger brain but not a larger body than their respective host. This finding underlines the importance of evaluating the role of cognitive abilities in exploitative relationships, both from the point of view of the exploiter and exploited.

The inclusion of food-stealing tactics in the foraging repertoire of birds can thus be seen as another expression of behavioural flexibility (Chapter 4). If we consider kleptoparasitism as a form of social intelligence, we can suggest that technical and social intelligence have evolved together. Indeed, large-brained birds and primates use tools, invent novel foraging techniques, learn quickly (reviewed in Lefebvre et al. 2004) and engage in deceptive (primates; Byrne & Corp 2004) or exploitative acts (birds; Chapter 4). It is still not clear which selective pressures have been more determinant in favouring the evolution of encephalisation. What we can observe today, however, is that a large brain often allows considerable behavioural flexibility in both the social and ecological or technical domains (see also Shultz & Barton 2006), and that advances in one domain might open doors to advances in the other domain (e.g. use of tools in the social domain; Goodall 1986). Resource defence theory suggests that feeding peacefully in a group and aggressively defending solitary access to food are extremes on a continuum driven by the density and predictability of resources in space and time (Brown 1964; Grand & Grant 1994). If resource distribution also drives the variation between conservative specialisation and opportunistic generalism (e.g. higher behavioural flexibility), then the same ecological factors may be behind both social and technical intelligence. For example, experimentally making a feeding environment more unpredictable leads starlings to rely more on information coming from conspecifics (Rafacz & Templeton 2003), doves to feed in unaggressive groups rather than defend (Goldberg et al. 2001) and rodents to select a more generalist diet (Gray 1981). Social and non-social aspects of cognition may thus co-vary with similar ecological conditions. If this is so, then an animal that uses intelligent foraging techniques may also be an efficient social exploiter of others.

In this thesis, I focused on one particular food processing technique that is both an innovation and a proto-tool behaviour, dunking in Carib grackles of Barbados. In the field, dunking rates vary from 0 % to as high as 70 % depending on social and environmental conditions (Morand-Ferron, pers. obs.). Rates of food dunking varied with food characteristics, travel costs between food and water, density of conspecifics and risk of kleptoparasitism. The usually low rates of dunking in the wild thus seem to be due to low benefits and/or high costs of the technique in most field conditions. My observations did not support the view that dunking rates were limited by the ability of individual grackles to learn the behaviour, as almost all birds exhibited the technique in captivity. These conclusions suggest that the expression of intelligent behaviour should be studied in a suite of conditions examining each variable thought to influence its costs and benefits. Field observations will usually provide suggestions as to which variables should be tested (e.g. in the case of dunking, washing of soiled food and soaking of hard items had been suggested in ornithological reports on the behaviour in the common grackle, *Q. quiscula*). Captive observations will often be necessary to control efficiently for some variables such as the presence of potential exploiters, and to investigate cognitive processes involved in learning and performing the behaviour. The cost and benefit framework that has been so successful in behavioural ecology should be applied to the study of cognition, so that intelligent behaviour is not just seen as something an animal can or cannot do, but as something that yields or not a sufficient payoff to be expressed in a given situation.

References

Barash, D. P., Donovan, P. & Myrick, R. 1975. Clam dropping behavior of glaucous-winged gull (*Larus glaucescens*). Wilson Bulletin, 87, 60-64.

Barnard, C. J. 1984. The evolution of food-scrounging strategies within and between species. In: Producers and scroungers: strategies of exploitation and parasitism (Ed. by C. J. Barnard), pp. 95-126. New York: Chapman & Hall.

Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers - A general model and its application to captive flocks of house sparrows. Animal Behaviour, 29, 543-550.

Brown, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bulletin, 76, 160-169.

Bugnyar, T. & Kotrschal, K. 2002. Observational learning and the raiding of food caches in ravens, *Corvus Corax*: is it 'tactical' deception? Animal Behaviour, 64, 185-195.

Byrne, R. W. & Corp, N. 2004. Neocortex size predicts deception rate in primates. Proceedings of the Royal Society of London Series B-Biological Sciences, 271, 1693-1699.

Byrne, R. W. and Whiten, A. 1988. Machiavellian intelligence: social expertise and the evolution of intellect in monkeys, apes and humans. Oxford: Clarendon Press.

Caldwell, C. A. & Whiten, A. 2003. Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*. Animal Behaviour, 65, 1085-1092.

Cooper, S. M. 1991. Optimal hunting group size - The need for lions to defend their kills against loss to spotted hyaenas. African Journal of Ecology, 29, 130-136.

Cristol, D. A. & Switzer, P. V. 1999. Avian prey-dropping behavior. II. American crows and walnuts. Behavioral Ecology, 10, 220-226.

Dally, J.M., Clayton, N.S. & Emery, N.J. 2006. The behaviour and evolution of cache protection and pilferage. Animal Behaviour, 72, 13-23.

Dekker, D. 2003. Peregrine falcon predation on dunlins and ducks and kleptoparasitic interference from bald eagles wintering at Boundary Bay, British Columbia. Journal of Raptor Research, 37, 91-97.

Drea, C. M. & Wallen, K. 1999. Low-status monkeys "play dumb" when learning in mixed social groups. Proceedings of the National Academy of Sciences of the USA, 96, 12965-12969.

Gajdon, G. K., Fijn, N. & Huber, L. 2006. Limited spread of innovation in a wild parrot, the kea (*Nestor notabilis*). Animal Cognition, 9, 173-181.

Galef, B. G., Marczinski, C. A., Murray, K. A. & Whiskin, E. E. 2001. Food stealing by young Norway rats (*Rattus norvegicus*). Journal of Comparative Psychology, 115, 16-21.

Giraldeau, L.-A. & Lefebvre, L. 1987. Scrounging prevents cultural transmission of food-finding behavior in pigeons. Animal Behaviour, 35, 387-394.

Goldberg, J. L., Grant, J. W. A. & Lefebvre, L. 2001. Effects of the temporal predictability and spatial clumping of food on the intensity of competitive aggression in the Zenaida dove. Behavioral Ecology, 12, 490-495.

Goodall, J. 1986. The chimpanzees of Gombe: patterns of behaviour. Cambridge: Belknap Press.

Goss-Custard, J. D., Cayford, J. T. & Lea, S. G. 1999. Vigilance during food handling by oystercatchers *Haematopus ostralegus* reduces the chances of losing prey to kleptoparasites. Ibis, 141, 368-376.

Grand, T. C. & Grant, J. W. A. 1994. Spatial predictability of food influences its monopolization and defense by juvenile convict cichlids. Animal Behaviour, 47, 91-100.

Gray, L. 1981. Genetic and experiential differences affecting foraging behavior. In: Foraging behavior: ecological, ethological and psychological approaches, (Ed. by A. C. Kamil and T. D. Sargent), pp. 455-473. Garland: New York.

Hamilton, I. M. & Dill, L. M. 2003. Group foraging by a kleptoparasitic fish: a strong inference test of social foraging models. Ecology, 84, 3349-3359.

Lefebvre, L. & Helder, R. 1997. Scrounger numbers and the inhibition of social learning in pigeons. Behavioural Processes, 40, 201-207.

Lefebvre, L., Reader, S. M. & Sol, D. 2004. Brains, Innovations and Evolution in Birds and Primates. Brain Behavior and Evolution, 63, 233-246.

Ottoni, E. B., De Resende, B. D. & Izar, P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Animal Cognition, 8, 215-219.

McKechnie, A. M., Smith, A. T. & Peacock, M. M. 1994. Kleptoparasitism in pikas (*Ochotona pinceps*) - Theft of hay. Journal of Mammalogy, 75, 488-491.

Rafacz, M. & Templeton, J. J. 2003. Environmental unpredictability and the value of social information for foraging starlings. Ethology, 109, 951-960.

Reader, S. M. & Laland, K. N. 2003. Animal innovation. Oxford: Oxford University Press.

Robinette, R. L. & Ha, J. C. 2001. Social and ecological factors influencing vigilance by Northwestern crows, *Corvus caurinus*. Animal Behaviour, 62, 447-452.

Shultz, S. & Dunbar, R. I. M. 2006. Both social and ecological factors predict ungulate brain size. Proceedings of the Royal Society of London Series B-Biological Sciences, 273, 207-215.

Stahler, D., Heinrich, B. & Smith, D. 2002. Common ravens, *Corvus corax*, preferentially associate with grey wolves, *Canis lupus*, as a foraging strategy in winter. Animal Behaviour, 64, 283-290.

Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D. 2001. Do woodpecker finches acquire tool-use by social learning? Proceedings of the Royal Society of London Series B-Biological Sciences, 268, 2189-2193.

Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M. 2002. The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). Ecology Letters, 5, 656-664.

Temeles, E. J. 1990. Interspecific territoriality of Northern harriers - The role of kleptoparasitism. Animal Behaviour, 40, 361-366.

Vickery, W. L., Giraldeau, L. A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991. Producers, scroungers, and group foraging. American Naturalist, 137, 847-863.

Whiteley, J. D., Pritchard, J. S. & Slater, P. J. B. 1990. Strategies of mussel dropping by carrion crows *Corvus corone corone*. Bird Study, 37, 12-17.

Appendix I.

Dunking behaviour in wild American crows[1]

---

[1] Reprinted from Wilson Bulletin, vol. 117, Morand-Ferron, J., Dunking behavior in American crows, pp. 405-407, Copyright (2005), with permission from Wilson Journal of Ornithology.

Dunking behaviour, the immersion of food items in water, is a relatively rare behaviour in free-ranging birds, with fewer than 40 species reported to dunk in the field (Morand-Ferron et al. 2004). Prevalent among these records are members of the genera *Quiscalus* (five species out of six) and *Corvus* (seven species out of 43). In this paper, I describe dunking behaviour in another corvid species, *Corvus brachyrhynchos*. Although well-known among naturalists (C. Caffrey pers. obs.), dunking behaviour had not been reported before in American crows. Reports of unusual behaviours are useful in estimating the taxonomic distribution of innovative behaviour, which can be used to test predictions in neurobiology, ecology, evolution, and cognition (Reader & Laland 2003).

On 21 September 2003, at 11:00 EST, I observed a single crow pick up in its bill two pieces of dry white bread (3 x 3 cm) thrown on the ground near the entrance of the Lac-aux-castors section of Mont-Royal Park in Montréal, Québec, Canada. The bird then flew away to a nearby (10 m) rain puddle and dunked the food in it twice before eating it on the spot. On 23 September, I returned to the park, and again witnessed the dunking of bread by a free-ranging crow, this time 500 m further from the entrance. Between September 23 and October 16, I observed at least three different individuals (birds were not marked but sometimes dunked almost simultaneously in different puddles) dunking fresh and dry bread, and peanuts in the shell. I also observed crows eating dry dog-food pellets (n = 16), maraschino cherries (n = 2) and live crickets (n = 6) placed 8 m from the nearest rain puddle, but I observed no dunking of these items (all reported to be dunked by other species; see table in Morand-Ferron et al. 2004).

It is difficult to determine the function of dunking behaviour in wild American Crows from these observations. Among the different functions suggested for birds, the use of food as a sponge in order to bring water to nestlings (Koenig 1985) can be ruled out because the events I observed occurred many weeks after juveniles had left the nest. Washing of soiled food (Simmons 1950; Watkin 1950; Caldwell 1951; Jordheim 1965; Wible 1975; Johnson 1976; Seibt & Wickler 1978; Vader 1979; Zach 1979; Schardien & Jackson 1982; del

Hoyo et al. 1996; Henry et al. 1998) also may be ruled out because the food items were soiled during the process of dunking clean food into muddy rainwater.

I conducted two field experiments with bread and peanuts to examine two possible determinants of dunking: the effect of item size on the dunking frequency of bread and the advantage that dunking might offer in softening peanut shells, making them easier to open. In the first set of trials, I tested the hypothesis that dunking of hard food would be more prevalent with items that are too large to be swallowed without breaking them into pieces than with smaller items. I provided the crows ($n = 3$) at Mont-Royal Park with two sizes of dry bread: small (2 x 2 cm, $n = 16$) and large (4 x 4 cm, $n = 17$). I ran one trial per day between 10:00 and 12:00 on four days in October 2003. For each trial, I recorded the behaviour of crows with six to ten pieces of bread, throwing one piece at a time on the ground and alternating between the two sizes each time. I noted whether the crow that took the piece dunked it in a nearby puddle (8 m distance) or ate it dry. A chi-square test revealed that the large pieces were dunked more often than the small ones (58.8 versus 18.8 % respectively; $\chi^2 = 5.53$, d.f. = 1, $p = 0.014$). This result suggests that the size of food items might influence the frequency of dunking behaviour in birds.

In the second set of trials, I tested the hypothesis that crows dunking peanuts could accelerate the opening process by softening the shell in water. This potential advantage in reduced handling time must be distinguished from the possibility that dunking peanuts would lubricate them and allow the birds to swallow them whole. I observed the latter once in ring-billed gulls, *Larus delawarensis* who have also been reported dunking crackers (Stokes & Stokes 1985), but not in crows, who never ate the shell. On four days between 26 September and 16 October 2004 and four days between April 7 and April 14 2005 from 10:00 to 12:00, I provided peanuts in their shells near a rain puddle (8 m) to crows ($n = 5$ in 2004 and $n = 6$ in 2005) at Mont-Royal Park. On each day, I observed a similar amount of dunked and non-dunked peanuts for a total of four to eight peanuts per day. I defined shelling latency as the time it took to reach the second peanut inside a two-peanut shell, not including the time spent in locomotion. I discarded observations where the crow did not eat the second peanut but cached it in the grass ($n = 3$). On average, shelling latency was 55.1 ± 35.7 sec when the crows dunked ($n = 22$), and 65.4 ± 48.6 sec without dunking ($n = 26$), which is not significantly different ($t = 0.818$, d.f. = 46, $p = 0.417$). Dunking thus does not accelerate the shelling of peanuts. Crows sometimes dunked half-peanuts in water after having extracted them from the shell, which resulted in the removal of the skin. This behaviour has also been observed in common grackles, *Quiscula quiscula* (Wible 1975), and might explain why crows at Mont-Royal Park handled peanuts in water.

The function of dunking behaviour seems to vary depending on the species performing it and the item dunked. For example, raptors kill live prey by holding them under water (e.g. *Accipiter nisus*; Weekley 1997*)*. Shorebirds are mainly thought to wash muddy items by rinsing them in water before consumption (e.g. *Tringa hypoleucos*; Simmons 1950). Studies on Carib grackles (*Quiscalus lugubris*) have revealed that birds dunk more often dry bread than fresh bread (Morand-Ferron et al. 2004) and that dunking reduces handling time with hard items (Morand-Ferron et al., subm.). These results suggest that dunking in this population is a food-processing technique easing the ingestion of items that are otherwise difficult to swallow. Our observations on American crows dunking bread suggest a similar function to the behaviour. A peculiarity of corvid dunking behaviour seem to be its variability, with observations suggesting transportation of water to nestlings (*Corvus corax*; Hauri 1956), drowning of live prey (e.g. *Pica nuttalli*; Blackburn 1968), washing of soiled items (e.g. *Corvus caurinus*; Zach 1979) and softening of hard (*Corvus corone*; Goodwin 1986) and large items (*Corvus brachyrhynchos*; this study). Our observations add to the diversity of dunking reports in corvids and bring further support to the suggestion made by Goodwin (1986) that dunking may be a standard part of the feeding repertoire in the genus *Corvus*.

Acknowledgements

I would like to thank L. Lefebvre, C. Caffrey and two anonymous referees for helpful comments on a previous version of the paper. I am also grateful to E. Trottier for help in the field.

References

Blackburn, C. F. 1968. Yellow-billed magpie drowns its prey. Condor, 70, 281.

Caldwell, J. A. 1951. Food-washing in the water rail. British Birds, 44, 418.

del Hoyo, J., Elliott, A. & Sargatal, J. 1996. Handbook of the birds of the world, vol. 3. Barcelona: Lynx Edicions.

Goodwin, D. 1986. Crows of the world, 2nd ed. London: British Museum.

Hauri, R. 1956. Beitrage zur biologie des kolkraben (*Corvus corax*). Ornithologische Beobachtungen, 53, 28-35.

Henry, P.-Y., Bénéat, Y. & Maire, P. 1998. Redshank *Tringa totanus* feeding on young edible frogs *Rana kl. esculenta.* Nos Oiseaux, 45, 57-58.

Johnson, I. W. 1976. Washing of food by spotless crake. Notornis, 23, 357.

Jordheim, S. O. 1965. Unusual feeding behavior of yellowlegs. Blue Jay, 23, 25.

Koenig, W. D. 1985. Dunking of prey by Brewer's blackbirds: a novel source of water for nestlings. Condor, 87, 444-445.

Morand-Ferron, J., Lefebvre, L., Reader, S. M., Sol, D. & Elvin, S. 2004. Dunking behaviour in Carib grackles. Animal Behaviour, 68, 1267-1274.

Reader, S. M. & Laland, K. N. 2003. Animal innovation. Oxford: Oxford University Press.

Schardien, B. J. & Jackson, J. A. 1982. Killdeers feeding on frogs. Wilson Bulletin, 94, 85-87.

Seibt, U. & Wickler, W. 1978. Marabou storks wash dung beetles. Zeitschrift fur Tierpsychologie, 46, 324-327.

Simmons, K. E. L. 1950. Food-washing by common sandpiper. British Birds, 43, 229-230.

Stokes, D. & Stokes, L. 1985. Bird song (part II). Bird Watcher's Digest, 7, 54-59.

Vader, W. 1979. Cleptoparasitism on bar-tailed godwits by common gulls. Fauna, 32, 62-65.

Watkin, R. 1950. Food-washing by blackbird. British Birds, 43, 156.

Weekley, D. R. 1997. Eurasian sparrowhawk drowning Eurasian jay. British Birds, 90, 524-526.

Wible M. W. 1975. Food washing by grackles. Wilson Bulletin, 87, 282-283.

Zach, R. 1979. Shell dropping: decision-making and optimal foraging in Northwestern crows. Behaviour, 68, 106-177.

Appendix II.
Animal Use Protocols

Appendix III.

Permissions to include published material in the thesis