J Ethol (2007) 25:79–82
DOI 10.1007/s10164-006-0193-7

SHORT COMMUNICATION

Vincent Careau · Nicolas Lecomte · Jean-François Giroux
Dominique Berteaux

Common ravens raid arctic fox food caches

Received: October 27, 2005 / Accepted: January 16, 2006 / Published online: April 14, 2006

Abstract Cache recovery is critical for evolution of hoarding behaviour, because the energy invested in caching may be lost if consumers other than the hoarders benefit from the cached food. By raiding food caches, animals may exploit the caching habits of others, that should respond by actively defending their caches. The arctic fox (*Alopex lagopus*) is the main predator of lemmings and goose eggs in the Canadian High Arctic and stores much of its prey in the ground. Common ravens (*Corvus corax*) are not as successful as foxes in taking eggs from goose nests. This generalist avian predator regularly uses innovation and opportunism to survive in many environments. Here, we provide the first report that ravens can successfully raid food cached by foxes, and that foxes may defend their caches from ravens.

Key words *Alopex lagopus* · *Corvus corax* · Food caching · Cache raiding · Defence of food caches · Foraging innovation · Bylot Island

Introduction

Hoarding behaviour, a widespread foraging strategy in animals, entails two key processes – delayed consumption of the food and caching of food items to prevent consumption by other individuals (Vander Wall 1990). Cache recovery is a critical component of hoarding behaviour, because the benefits of hoarding decrease if consumers other than the hoarders recover cached food (Andersson and Krebs 1978). Cache raiding is a form of kleptoparasitism that is more likely to occur in open habitats, especially for systems involving birds, because they use visual cues to locate caches (Brockman and Barnard 1979).

In some Arctic goose breeding colonies, all factors are present for the behavioural evolution of both cache raiding and mechanisms aimed at reducing cache raiding. First, hoarding behaviour is usually more common at high latitudes because prey items such as goose eggs and lemmings are seasonally abundant (Smith and Reichman 1984). These resources can also be efficiently stored for later use, because of their small size, their natural packaging of skin or shell, and the cold temperature of cache sites. Second, Arctic tundra is an open habitat with 24 h daylight during summer, which favours cache raiding after visual cues.

Arctic foxes (*Alopex lagopus*) and common ravens (*Corvus corax*) are opportunist predators that forage on lemmings and goose eggs (Bêty et al. 2002; Elmhagen et al. 2000; Nelson 1934). Arctic foxes are efficient predators on lemmings and goose nests and cache a high proportion of the eggs they take (Samelius and Alisauskas 2000; Stickney 1991). Common ravens are less successful in preying upon lemmings and eggs but have a remarkable capacity to innovate foraging behaviour (Andersson 1989; Bêty et al. 2002; Ficken 1977; Heinrich 1995). Although cache raiding by ravens has been observed, it occurs mostly on caches made by other ravens (Bugnyar and Kotrschal 2002b). In a broad sense, an innovation is a new or modified learned behaviour not previously found in the population (Reader and Laland 2003). Foraging innovation is vital for species with generalist and opportunistic lifestyles, for example ravens, and can be further defined as the ingestion of a new food type or the use of a new foraging technique (Lefebvre et al. 1997). Here, we document the first report of common ravens raiding arctic fox food caches and foxes defending their caches against ravens.

V. Careau (✉) · J.-F. Giroux
Département des sciences biologiques and Groupe de recherche en écologie comportementale et animale, Université du Québec à Montréal, P.O. Box 8888 Stn Centre-ville, H3C 3P8 Montréal, QC, Canada
Tel. +1-514-9873000 (7645); Fax +1-514-9874647
e-mail: careau.vincent@courrier.uqam.ca

V. Careau · D. Berteaux
Chaire de recherche du Canada en conservation des écosystèmes nordiques and Centre d'études nordiques, Université du Québec à Rimouski, 300 Allée des Ursulines, G5L 3A1 Rimouski, QC, Canada

N. Lecomte
Département de biologie and Centre d'Études Nordiques, Université Laval, G1K 7P4 Québec, QC, Canada

Materials and methods

Our observations were made on Bylot Island in the Canadian High Arctic (72°53′N, 79°54′W) from June 8 to July 20 in 2004 and 2005. The mean daily temperature during the observation period was 3.7°C (1.0–7.7°C) and the mean daily precipitation was 1.7 mm (0–15 mm). Bylot Island is the primary breeding site for greater snow geese (*Chen caerulescens atlantica*; Reed et al. 2002). Nesting density of other land birds is low compared with that of geese (Lepage et al. 1998). Although we found no raven nest, they are known to breed in the study area (B. Audet and O. Gilg, personal communication). The weight, width, and length of greater snow goose eggs range from 85–145 g, 4.8–5.6 cm, and 7.3–8.9 cm, respectively ($n = 60$; V. Careau, unpublished data). Both brown (*Lemmus sibiricus*) and collared (*Dicrostonyx groenlandicus*) lemmings occur on Bylot Island. The abundance of brown lemmings varies in cycles of large amplitude with peaks every 3–4 years, which affects arctic fox breeding success (Gauthier et al. 2004). Lemming abundance was high in 2004 (peak year) and low in 2005 (declining phase, snap-trap census; G. Gauthier, personal communication). The main goose colony encompassed 16 km^2 with a mean density of 206 nests km^{-2} during the study (N. Lecomte, unpublished data) and was located in gently slopping hills of mesic tundra and wetlands. We made observations from two blinds and covered an area of 3.4 km^2 using spotting scopes, 20–60×. Foxes were identified by ear tags and/or the distinctive pattern of their pelts, recognition of which was facilitated by their shedding from winter to summer pelage. We counted common ravens inside the observation area for 10 min every second day. We performed focal sampling of foxes foraging in the goose colony and recorded all interactions between foxes and ravens using a digital voice recorder.

Results

We conducted 549 h of observation over 66 days (2004: 29 days, 2005: 37 days) during which we recorded 82 h of arctic fox foraging activity. At least 5 and 7 different adult foxes were frequently seen foraging in the area in 2004 and 2005, respectively. Ravens were present on 30 of 35 counting periods (mean = 4 individuals, range 1–30, median = 3) and we detected them flying over or perching on top of the adjacent hills on 14 occasions during focal fox observations. During the entire study we observed foxes caching 169 eggs and 30 lemmings; ravens were present during 10 (5%) of these caching events. On two occasions a fox carrying an egg was followed by a raven walking at a distance of approximately 20 m. In both instances, the animals went out of the observation limit after 5 min with the fox still carrying the egg.

We witnessed five interactions between ravens and foxes involved in food caching, raiding, and defending (Table 1). On two occasions, we observed a raven raiding a food item that had been cached by a fox few minutes previously. On 24 June 2004 at 20:30, on a sunny evening, a fox spent 18 s caching a lemming. While the fox was caching its food, two ravens landed about 15 m away. Immediately after the fox had left the cache and was hunting for other lemmings about 40 m away, both ravens walked directly towards the cache, probing the ground as they approached. One of the ravens retrieved the lemming 121 s after starting its search and took off with the lemming in its beak. The second bird followed. We could not tell whether or not the lemming cached by the fox had been partly visible to the ravens. The second observation of cache raiding by ravens occurred on 8 June 2005, at 16:00, on a sunny afternoon. An arctic fox cached a goose egg in the snow that covered 90% of the study area at this date. Approximately 10 s after the fox had left the cache, and was about 50 m away, a raven arrived from the opposite direction and landed at the cache site. Immediately upon landing, it retrieved the egg and flew off with it in its beak. It is likely the raven was able to detect the cache because the fox had disturbed the snow surface where the egg was cached and left tracks leading to and from the cache.

Foxes did not attempt to defend their caches in either of the successful raids made by ravens. On three other occasions, however, we observed two different individuals defending their cached food. First, on 15 June 2005 at 19:20, we observed a fox spending 40 s caching an egg before spotting a raven on the ground at a distance of 15 m. In a two-minute period the fox charged the raven four times, but was unsuccessful at making it leave the area. Between charges the fox returned to the cache site and lay down for 3 min at a distance of one meter from the cache until the raven flew off at 19:25. The fox left the site one minute after the raven flew away and neither was seen again by the end of the observation period, 95 min later. Another observa-

Table 1. Interactions between arctic foxes and common ravens during caching, cache-raiding, and cache-defending events on Bylot Island, Nunavut, 2004 and 2005

Date	Time	Food item cached by the fox	Number of ravens attending	Landing distance from cache (m)	Time between fox leaving and cache raiding (s)	Time the fox spent defending the cache (min)	Raiding successful
24 June 2004	20:30	Lemming	2	15	121	–	Yes
8 June 2005	16:00	Goose egg	1	0	10	–	Yes
15 June 2005	19:20	Goose egg	1	15	–	6	No
27 June 2005	20:10	Goose egg	1	20	–	46	No
7 July 2005	17:32	Goose egg	1	15	–	8	No

tion of a fox defending its food cache from a raven was made 27 June 2005, at 20:10, on a sunny evening. A fox spent 53 s caching an egg in the ground. While the fox was digging, a raven landed 20 m away. After burying its egg the fox moved approximately 30 m away from the cache in ca. 40 s. It then spotted the raven and returned to the cache. Using its snout, the fox spent 262 s raking more leaves and moss on top of the cache. It then lay down beside the cache and stayed there for 13 min until the raven flew away at 20:30. The fox left the area 28 min after the raven. Neither the fox nor the raven was observed at the cache during the remaining 5 h of observation. The same fox defended a second cache on 7 July 2005, at 17:32, on a sunny afternoon. The fox spent 39 s caching an egg in the ground. A raven landed on a mound 15 m away 6 s before the fox had finished storing the egg. The fox noticed the bird when leaving the site, prowled the area for 15 s and charged the raven for 21 s. The raven flew off but remained near (<20 m) the cache until 17:40. After the initial charge, the fox returned to its cache and lay down nearby until 17:41. Neither the fox nor the raven returned to the site during the remaining 110 min of observation. Other than these three occasions, we never observed foxes staying at the cache site after storing food items.

During our study, we often observed ravens probing the ground with their beaks while walking on the tundra. On 23 June 2005 at 20:30, a raven landed in the observation area, walked for approximately 5 m, spent 5 s removing moss with its beak, and recovered a cached egg. No fox or raven had been observed in the area during the previous two hours of observation. After spending 4 min eating the egg, the raven walked 150 m to another cache site and recovered another egg. The bird flew off with the egg in its beak in the direction from which it had originally come. In more than 900 h of observation, we have never observed ravens caching goose eggs (this study and Bêty et al. 2001, 2002). The only items cached by ravens on Bylot Island were experimental plastic eggs used for another study. These may have been cached because ravens were unable to break and eat them.

Discussion

To the best of our knowledge, this is the first report of common ravens (alone or in pairs) raiding arctic fox food caches. We argue that the interspecific cache-raiding behaviour of ravens is a foraging innovation that enables them to exploit goose eggs more efficiently. The greater snow goose population has increased from a few thousand in the early 1900s to 50,000 in 1965, and to an estimated 700,000 in 2004 (Gauthier et al. 2005). This 14-fold growth in the last 40 years has obviously increased the number of eggs available to predators throughout the goose breeding range, which in return has probably increased the number of eggs cached by foxes. Arctic foxes can acquire 19–88% of the goose eggs produced annually on Bylot Island (Bêty et al. 2002); of these approximately 80% are cached (V. Careau, unpublished data). In another goose colony on Banks Island, individual foxes were observed to cache up to 1,000 eggs per summer (Samelius and Alisauskas 2000). Foraging innovations enabling ravens to benefit from the increased abundance of goose eggs should be strongly selected for.

Corvids has been observed raiding food caches made by canids in other circumstances. Bugnyar and Kotrschal (2002a) observed wild ravens raiding food caches made by captive wolves (*Canis lupus*). As observed in our study, potential raiders perched close to the wolves that were caching and waited until they moved away before approaching the cache. Similarly, Henry (1986) reported that magpies (*Pica pica*) attempted to raid food caches immediately after they were made in the snow by a red fox (*Vulpes vulpes*). In response to raiding of food caches, hoarders may alter their behaviour to prevent their caches from being detected by kleptoparasites. Macdonald (1976) observed that when a well fed hand-reared red fox became careless in making its caches, the food was almost invariably raided by corvids. On the day after it lost all its stored food to crows (and on which it did not eat because of this) the fox began to cache carefully again, however. All these observations including ours suggest that the kleptoparasitic behaviour of corvids exerts a pressure on foxes to carefully conceal their cached food.

Visual observation is essential for common ravens to achieve conspecific cache raiding (Bugnyar and Kotrschal 2002a). By following foxes carrying eggs, ravens can enhance their raiding efficacy by acquiring visual information about cache location. Henry (1986) suggested that red foxes could deter corvids by carrying food items until the birds give up. This could also be true for the arctic foxes we saw moving away with an egg followed by a raven for more than 5 min.

There is no previous report of foxes chasing, defending, or guarding cached food items against ravens. In response to cache defence, ravens may attempt to remain undetected by foxes and delay cache raiding until the fox cannot actively defend it (Bugnyar and Kotrschal 2002a). Our observation of a raven recovering two cached eggs long after the fox had left them supports this hypothesis. To raid cached food, ravens may conceal themselves when they see a fox caching, remember the cache location, and return later for raiding. Probing the ground as they walk on the tundra may also help ravens to find food caches. We do not yet know whether they concentrate their searches in areas where they have previously observed foxes caching food, however. The behavioural evolution of such a natural system of hoarders and raiders and the cognitive strategies employed warrant further investigation and experimental research.

Acknowledgements Thanks to Gabrielle Darou and Ambroise Lycke for field assistance. We are indebted to the Hunters and Trappers Association of Pond Inlet, Nunavut Territory, for assistance and support. VC is grateful to the Mountain Equipment Coop for providing material and to Sanimal for a scholarship. Université Laval and the Centre d'Études Nordiques provided financial assistance to NL. Funding and support were provided by the Polar Continental Shelf Project, Fonds Québécois de la Recherche sur la Nature et les Technologies,

the Nunavut Wildlife Management Board, the Natural Sciences and Engineering Research Council of Canada, Canada Network of Centres Excellence ArcticNet, and the Canada Research Chair Program. We thank Luc Alain Giraldeau, Denis Réale, Louis Lefebvre, and the Groupe de Recherche en Écologie Comportementale et Animale (GRÉCA) for fruitful discussions and Heather Bryan for proofreading. We are grateful to two anonymous referees for constructive comments on the manuscript. This is Polar Continental Shelf Project contribution no 01905.

References

Andersson M, Krebs J (1978) On the evolution of hoarding behaviour. Anim Behav 26:701–707

Andersson S (1989) Tool use by the fan-tailed raven (*Corvus rhipidurus*). Condor 91:999–999

Bêty J, Gauthier G, Giroux J-F, Korpimäki E (2001) Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388–400

Bêty J, Gauthier G, Korpimäki E, Giroux J-F (2002) Shared predators and indirect trophic interactions: lemming cycles and arctic-nesting geese. J Anim Ecol 71:88–98

Brockman HJ, Barnard CJ (1979) Kleptoparasitism in birds. Anim Behav 27:487–514

Bugnyar T, Kotrschal K (2002a) Observational learning and the raiding of food caches in ravens, *Corvus corax*: is it "tactical" deception? Anim Behav 64:185–195

Bugnyar T, Kotrschal K (2002b) Scrounging tactics in free-ranging ravens, *Corvus corax*. Ethology 108:993–1009

Elmhagen B, Tannerfeldt M, Verucci P, Angerbjorn A (2000) The arctic fox (*Alopex lagopus*): an opportunistic specialist. J Zool 251:139–149

Ficken MS (1977) Avian play. Auk 94:573–582

Gauthier G, Bêty J, Giroux JF, Rochefort L (2004) Trophic interactions in a high arctic goose colony. Integr Comp Biol 44:119–129

Gauthier G, Giroux JF, Reed A (2005) Interactions between land use, habitat use and population increase in greater snow geese: what are the consequences for natural wetlands? Global Change Biol 11:856–868

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

Heinrich B, Pepper JW (1998) Influence of competitors on caching behaviour in the common raven, *Corvus corax*. Anim Behav 56:1083–1090

Henry JD (1986) Red fox: the catlike canine. Smithsonian Institution Press, Washington

Lefebvre L, Whittle P, Lascaris E, Finkelstein A (1997) Feeding innovations and forebrain size in birds. Anim Behav 53:549–560

Lepage D, Nettleship DN, Reed A (1998) Birds of Bylot Island and adjacent Baffin Island, Northwest Territories, Canada, 1979 to 1997. Arctic 51:125–141

Macdonald DW (1976) Food caching by red foxes and some other carnivores. Z Tierpsychol 42:170–185

Nelson AL (1934) Some early summer food preferences of the American raven in southeastern Oregon. Condor 36:10–115

Reader SM, Laland KN (2003) Animal Innovation. Oxford University Press, Oxford

Reed A, Hughes RJ, Boyd H (2002) Patterns of distribution and abundance of Greater Snow Geese on Bylot Island, Nunavut, Canada 1983–1998. Wildfowl 53:53–65

Samelius G, Alisauskas RT (2000) Foraging patterns of arctic foxes at a large arctic goose colony. Arctic 53:279–288

Smith CC, Reichman OJ (1984) The evolution of food caching by birds and mammals. Annu Rev Ecol Syst 15:329–351

Stickney A (1991) Seasonal pattern of prey availability and the foraging behavior of arctic foxes (*Alopex lagopus*) in a waterfowl nesting area. Can J Zool 69:2853–2859

Vander Wall SB (1990) Food hoarding in animals. University of Chicago Press, Chicago