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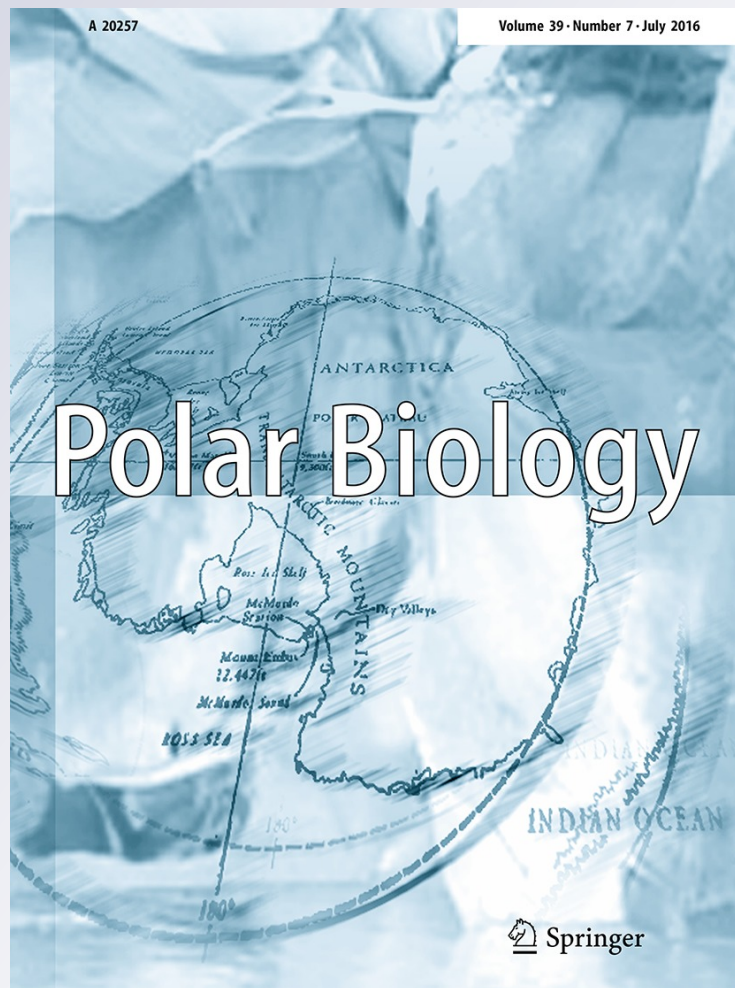
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Predation of arctic fox (*Vulpes lagopus*) pups by common ravens (*Corvus corax*)

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Abstract Identifying correctly trophic interactions is important for understanding population dynamics and ecosystem functioning. However, some predator–prey relationships may still remain undetected, due to the difficulty of observing rare predation events. We report the first observation of predation of arctic fox (*Vulpes lagopus*) pups by common ravens (*Corvus corax*). The predation event was witnessed on Bylot Island, Nunavut, Canada, through an automatic camera placed on a den. On June 8, 2013, the day following pup emergence from the den, the complete litter of four was killed and taken away by a pair of ravens despite the intermittent presence of the mother. This event lasted 2.5 h, occurred during a low lemming year, and resulted in the fox pair failing their reproduction. Only two other fox litters were present that summer in our 600 km² study area, so this litter predated by ravens accounted for 25 % (4/16) of the pups produced. Our report shows how continuous monitoring of dens using automatic cameras can allow documentation of rare events. In addition to food competition and cache raiding, pup predation contributes to the antagonistic interactions between arctic foxes and ravens in the High Arctic, which may intensify

during low lemming years. This observation allows a better understanding of species interactions within the Arctic predator guild.

Keywords Interspecific killing · Juvenile · Predation · Foraging innovation · *Vulpes lagopus* · *Corvus corax*

Introduction

Animal population dynamics is shaped by key life history traits, including reproductive success, adult and juvenile survival (Stearns 1992; Williams et al. 2002). Those in turn are influenced by, e.g., environmental conditions (Anctil et al. 2014) and trophic interactions (Potapov 1997; Angerbjörn et al. 2004). In particular, predation can strongly affect recruitment of juveniles (Gaillard et al. 1998; Morrisette et al. 2010). Identifying correctly predator–prey relationships is thus important for understanding trophic interactions and population dynamics, and, in this context, the simplified ecosystems found in polar environments allow productive testing of hypotheses in trophic and community ecology (Legagneux et al. 2012, 2014).

The arctic fox (*Vulpes lagopus*) is a relatively common predator within its arctic circumpolar distribution, where its generalist feeding regime impacts the state of the tundra ecosystem (Ehrich et al. 2015). It forms socially monogamous pairs which breed once a year using underground dens for the protection of the young (Angerbjörn et al. 2004). Pup emergence from the den is a critical life history event since pups are still weak and naïve at this stage, and thus vulnerable to predation (Gese 2001; Tannerfeldt et al. 2003). Both pair mates provide parental care during summer (Strand et al. 2000; Angerbjörn et al. 2004), yet pup

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mortality due to starvation (Tannerfeldt et al. 1994; Angerbjörn et al. 2004) and predation (Garrott and Eberhardt 1982; Meijer et al. 2011) can be relatively high. Reported predators of arctic foxes include red foxes (*Vulpes vulpes*), wolves (*Canis lupus*), wolverines (*Gulo gulo*), grizzly bears (*Ursus arctos*), gyrfalcons (*Falco rusticolus*), golden eagles (*Aquila chrysaetos*), white-tailed eagles (*Haliaeetus albicilla*), snowy owls (*Bubo scandiaca*), jaegers (*Stercorarius* spp.) and large hawks (*Buteo* spp.) (Garrott and Eberhardt 1982; Frafjord et al. 1989; Tannerfeldt et al. 2002; Booms and Fuller 2003; Cypher 2003). This list may not be exhaustive, due to the logistic challenges of observing rare predation events occurring specifically around pup emergence. As in any other research area of polar biology, however, it is likely that technological advances will allow rapid progress of knowledge and, more specifically, will help uncovering rare and undetected processes such as predator–prey relationships impacting arctic fox survival and breeding success.

Using systematic den monitoring of an arctic fox population through infrared automatic cameras, we describe the first observation of a predation event by common ravens (*Corvus corax*) on arctic fox pups at their den, despite the defense provided by one parent.

Materials and methods

We worked in a 600 km² area in the south plain of Bylot Island (73°N, 80°W), Nunavut, Canada, where the arctic fox population is monitored systematically since 2003 (Gauthier et al. 2013). The arctic fox is the main terrestrial predator of the area and feeds preferentially on two lemming species, the brown lemming (*Lemmus trimucronatus*), which shows 3–4-year cycles of abundance, and the collared lemming (*Dicrostonyx groenlandicus*), present at low density (Gruyer et al. 2008). During summer, a large breeding colony of Greater snow geese (*Chen caerulescens atlantica*) is also present and provides foxes with their main alternative prey (Gauthier et al. 2013). Other top predators, the red fox, the snowy owl, the rough-legged hawk (*Buteo lagopus*) and the peregrine falcon (*Falco peregrinus*), are rare and generally present only when lemming densities are high.

Fox dens were mapped in 2003 (Szor et al. 2008), and a total of 109 dens were monitored in 2013, when the reported predation event took place. Dens showing signs of activity (digging, hairs, tracks, prey remains, presence of adults or pups) in May were monitored until the end of July using infrared automatic color cameras (Silent Image PM35C31, RapidFire Professional PC85, and HyperFire PC800; Reconyx, Holmen, WI, USA). Cameras took a

series of five pictures without time interval each time a movement was detected, and series of pictures could follow each other without interruption. Visual observations of dens were also performed at breeding dens in July. Adult and young foxes were captured and ear-tagged (Rototags, Dalton Supplies Ltd., Henley-on-Thames, UK) as described in Tarroux et al. (2010). Based on rodent trapping during summer, the lemming density in 2013 was the lowest recorded in the study area since 2004 (Fauteux et al. 2015). Two ravens were involved in the event described here. We refer to them as raven A and raven B based on their order of apparition and their behaviors (Verbeek et al. 1994; Carere et al. 2005; Barnett et al. 2013). Both adults of the breeding pair using the den were tagged.

Results

Among the 109 arctic fox dens monitored in 2013, 65 showed signs of fox activity and thus received at least one automatic camera in May. Pup emergence occurred at only three dens, all located inside the snow goose colony. The predation event by the ravens occurred on June 8, 2013, at den 107, a 7 m × 13 m den composed of 17 burrows and located on a sand mound in mesic tundra, 1270 m from the sea coast. Most of the den was covered by short dry grass, and snow had already melted (Fig. 1), although ca. 75 % of the landscape was still snow-covered. According to camera sensors and picture interpretation, air temperature was around 15 °C, with no precipitation.

Two pups were seen for the first time on the den in the afternoon of June 7, 2013. The whole litter of four emerged early the next morning, whereas all subsequent events described here occurred during the afternoon of that same day (see Table 1 for a detailed chronology of events, and Fig. 1 for selected pictures showing the predation event). At 15:46:15, a raven visited the den but flew away as it was charged by the female arctic fox (Fig. 1a). The fox left the den at 15:51:23, and 2 min later, a raven (likely the one visiting earlier, hereafter raven A) landed on the den and took a goose egg located on the den near the pup present on the den at that time. At 15:57:13, raven A observed the pup closely and circled around it during 37 s, making short vertical leaps at least five times, before pecking the pup for the first time and likely killing it. A second raven (hereafter raven B) arrived at 15:58:28 and walked around raven A, who consumed the pup during 2 min and 9 s. No other pups were present on the den during the killing of the first pup. The return of the female fox on the den at 16:05:37 chased the ravens a second time. At 16:33:12, two pups were seen alive on the den with their mother (Fig. 1b). The female fox left the den at 16:33:12. Raven A killed the second pup at 16:49:51 (pup 2 is seen on Fig. 1c–e) and the

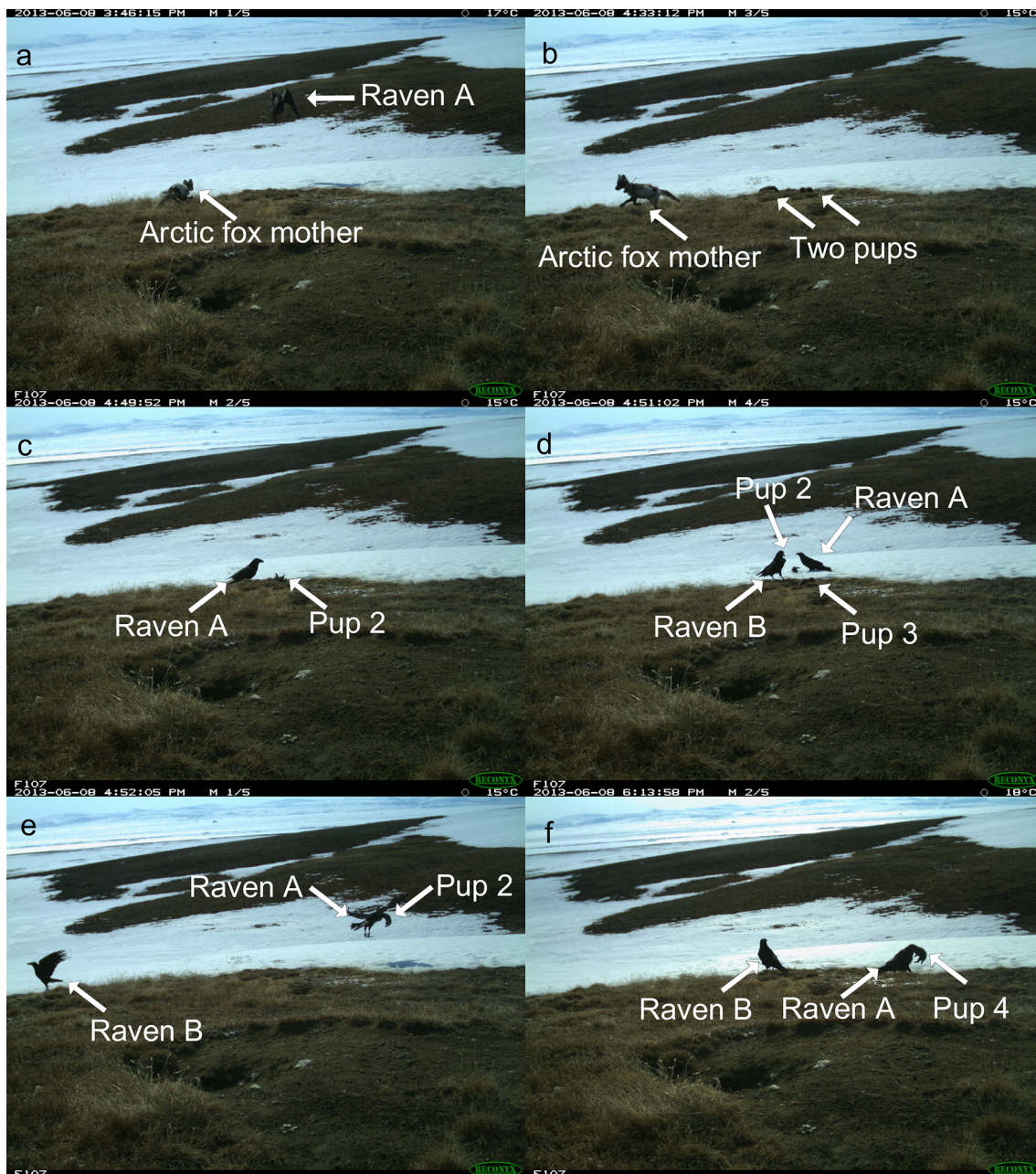


Fig. 1 Pictures taken by an automatic camera placed on an arctic fox (*V. lagopus*) den at Bylot Island (Nunavut, Canada), and showing the partial chronology of a predation event by ravens (*C. corax*) on arctic fox pups on June 8, 2013. **a** 15:46:15, the female arctic fox chases a

raven away from the den, **b** 16:33:12, the female and two very small pups walk on the den, **c**, **d** 16:49:52 and 16:51:02, raven A is feeding on a pup, **e**, **f** 16:52:05 and 18:13:58 raven A is carrying pups away from the den

third pup at 16:53:46 (pup 3 is seen on Fig. 1d). The female fox returned to the den after the killing of the second and third pups, but prior to the predation on the fourth pup. The ravens returned to the den at 18:12:03, 2 min after the female fox had left the den again, and killed the fourth pup at 18:12:34 (dead pup 4 is seen on Fig. 1f). Raven A observed closely the second pup during 31 s before killing it, but this observation period lasted

only 18 s for the fourth pup (no estimate available for the third pup). Raven B observed the scene without taking part in killings (Fig. 1d–f) and appeared less confident around pups. No other pup was observed at the den after the predation event. The full picture sequence, consisting of 575 pictures taken on June 8, 2013, from 15:45:02 to 20:45:57, is available in the online supplementary material (Online Resource 1).

Table 1 Chronology of the main events describing the predation of four arctic fox (*V. lagopus*) pups by two ravens (*C. corax*) on an arctic fox den observed through automatic cameras in June 2013 on Bylot Island, Nunavut, Canada

Date	Time	Event	Figure no.
June 7, 2013	14:56:35	2 pups emerge from the den	
June 8, 2013	06:12:40	4 pups on the den	
–	15:46:15	Female arctic fox chases a raven away from the den	1a
–	15:51:23	Female arctic fox leaves the den	
–	15:53:45	Raven A takes an egg next to pup 1	
–	15:57:13	Raven A observes pup 1	
–	15:57:50	Raven A kills pup 1	
–	15:58:28	Raven B arrives; Raven A consumes pup 1	
–	16:05:37	Female arctic fox carries a goose egg to the den; Ravens fly away	
–	16:08:04	Female arctic fox leaves the den	
–	16:32:04	Female arctic fox carries a goose egg to the den; 2 pups come out of the den	
–	16:33:12	Female arctic fox leaves the den; 2 pups are still on the den	1b
–	16:49:20	Raven A next to pup 2	
–	16:49:51	Raven A kills pup 2	1c
–	16:50:59	Raven B arrives	
–	16:51:02	Raven A consumes pup 2; Raven B observes pup 3	1d
–	16:52:05	Raven A leaves with pup 2 in its beak	1e
–	16:53:46	Raven A kills pup 3	
–	16:55:35	Raven A leaves with pup 3 in its beak	
–	18:06:55	Female arctic fox carries a goose egg to the den	
–	18:10:10	Female arctic fox leaves the den	
–	18:12:03	Raven B arrives	
–	18:12:16	Raven A next to pup 4	
–	18:12:34	Raven A kills pup 4	
–	18:13:58	Raven A carries pup 4 in its beak	1f
–	20:45:53	Female arctic fox carries a goose egg to the den	

Discussion

Although common ravens are cited as potentially preying on canid pups (Moore and Collins 1995; Latham and Boutin 2011), to our knowledge, this is the first report of such an event, indicating that we likely described a very rare but yet important behavior. Predation by ravens on arctic fox pups is highly unusual on Bylot Island; between 2008 and 2013, automatic cameras took 1,473,000 pictures at arctic fox dens, including 81 dens where fox litters were detected. In addition, 1196 h of visual observations were performed at selected breeding dens from 2008 to 2013. Yet, no other predation of fox pups by ravens was observed. We first explore several complementary hypotheses potentially explaining our observation [(1) intensive camera monitoring, (2) low lemming densities, (3) parental experience of the arctic fox pair] and then discuss several consequences [(1) further understanding of

raven behavior, (2) population-level impact for foxes, (3) trophic ecology of the arctic tundra].

Predation on arctic fox pups is often difficult to detect considering it usually occurs very fast and predators may carry the carcass away from the den (as did the raven in this note). In addition, the identity of the predators often has to be inferred from indices, such as feathers, left at the den or from the type of wound inflicted (Garrott and Eberhardt 1982). Automated cameras triggered by movements have become more sophisticated, reliable and cost-effective in recent years (McCallum 2013). The continuous monitoring of all active dens using cameras every summer in our study area thus increases considerably the probability of observing rare predation events on canid pups. Along with the clear identification of the predator, automated cameras can record the timing, duration and behaviors during the event, thereby providing valuable information on species interactions.

Ravens are opportunistic predators and scavengers. In the Arctic, they feed mostly on small rodents and complement their diet with scavenged items, such as carrion left by larger predators (Temple 1974). They can occasionally prey on animals larger than themselves (a raven weighs 900–1700 g, Johnston and Williamson 1960), such as ringed seal neonates (*Phoca hispida*) (Lydersen and Smith 1989) or adult hares (*Lepus* spp.) (Kumlien 1879; Otto 1998). The very low lemming densities of the summer 2013 may have increased foraging time of arctic foxes and thus decreased investment of parents in pup defense (Strand et al. 2000). This may explain why the male was absent from the den during the predation event, and why the female did not stay although she knew ravens were around. Low lemming abundance may also have led hungry pups to emerge from the den at a more vulnerable stage than if they had been well fed. Most litters on Bylot Island emerge around mid-June (median date: 17 June; range: 2 June–2 July; D. Berteaux, unpublished data), thus supporting the hypothesis that the predated pups emerged relatively early. Arctic fox pups emerging at smaller body size may also be more vulnerable to avian predation (Meijer et al. 2011). Body mass of pups captured in our study area ($n = 265$) ranged from 340 to 2900 g (mean: 1312 ± 447 g SD), and although we could not weigh those involved here, they were no doubt at the very low end of this body mass gradient. We have many pictures from other dens with ravens observing larger pups without attacking them, confirming that pups have a restricted period of vulnerability. Finally, it is possible that low lemming densities have stimulated ravens to look for alternative prey, increasing the probability that they attacked fox pups.

In Sweden, arctic fox females breeding for the first time suffered higher pup predation by golden eagles than experienced females (Meijer et al. 2011). In our case, the female was a third-time breeder at this den, so the lack of experience of the mother cannot explain the predation event. The male was, however, a first-time breeder at this den. In arctic foxes, the respective role of the parents in antipredatory behavior is unknown. Both parents attend the litter and guard the den, although males may spend less time at the den compared to females (Strand et al. 2000; Cameron et al. 2011). While males may allocate less time at the den, they may, however, be more efficient at deterring predators. For example, males have been observed aggressively defending pups against red foxes, whereas females vocally warned but appeared to avoid direct contact (Frafjord et al. 1989; Rodnikova et al. 2011). The complete absence of the male during the predation by ravens may thus have contributed to their success.

In our study area, ravens have previously been observed raiding fox food caches (Careau et al. 2007). In our observation, the raven was observed taking a goose egg on

the den, an item that was most probably brought there by the foxes, before attempting to kill the first pup. This suggests that the raven may have initially been drawn to the den by eggs and then noticed the pups on the den. The raven appeared to decrease observation time before killing pups. The bird seemed uncomfortable with the first pup, as shown by its frequent vertical leaps backwards, a “jumping-jack” maneuver which is typical of ravens encountering novel food items (Heinrich 1988; Heinrich et al. 1995). No leaping occurred with the other pups, which may indicate that the bird learned to recognize the pups as potential food or that it had determined that they were harmless at that size. The second raven, which also observed pups and leaped but did not kill them, remained close to the other bird, suggesting they may be a pair. Ravens quickly develop new feeding habits and foraging techniques (Heinrich 1995; White 2005; Careau et al. 2007), and thus it is important to report this type of rare behavior and monitor its potential spread in the population through social learning (Fritz and Kotrschal 1999; Schwab et al. 2008). In a context of rapid environmental changes, monitoring unusual predatory events such as the one observed here may help to understand the origin of new feeding habits. We have assumed that raven A and raven B could be identified from their apparently distinct behavioral types. However, without clear morphological differences nor any individual marking, uncertainty exists about identification, and the above discussion about raven behavior should be taken with care.

As a result of raven predation, the breeding pair failed their reproduction that summer. Only three fox litters (including the one where the predation event occurred) were recorded in the study area the same year. For comparison, up to 30 litters can be counted in our study area during a high lemming density year (D. Berteaux, unpublished data). Apart from the litter that was predated, the two other litters produced 12 pups, of which seven were tagged and two were resighted as breeders the next year. Ravens thus caused the failure of 33 % of the litters (1/3) and predated 25 % of the pups (4/16) produced in the study area that summer. Even if our observation suggests an isolated event, the good survival of the few tagged pups may suggest that the impact of this behavior could be important during low lemming years.

Predation on pups adds to other antagonistic interactions reported between arctic foxes and ravens, namely competition for food and cache raiding (Bêty et al. 2002; Careau et al. 2007). Ravens are not abundant on Bylot Island (Lepage et al. 1998), but the impact of these interactions may require further investigation. Overall, despite its relatively limited number of species, the Arctic tundra predator guild displays complex interactions, including different levels of direct and indirect competition,

kleptoparasitism, adult and juvenile predation (Frafjord et al. 1989; Bêty et al. 2001; Pamperin et al. 2006; Stempniewicz and Iliszko 2010; Killengreen et al. 2012). Establishing a complete network of all species interactions is thus important for ecological modeling and allows a better understanding of ecosystem functioning.

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