RESEARCH ARTICLE

What does the fox say? Arctic fox vocalization and associated den behaviours

Kayla J. Buhler[1,2], Gustaf Samelius[3], Ray Alisauskas[4,5] & Emily Jenkins[1]

[1]Department of Veterinary Microbiology, Western College of Veterinary Medicine, University of Saskatchewan, Saskatoon, SK, Canada; [2]Department of Forestry and Field Studies, Inland Norway University of Applied Sciences, Koppang, Norway; [3]Snow Leopard Trust, Seattle, WA, USA; [4]Department of Biology, University of Saskatchewan, Saskatoon, SK, Canada; [5]Prairie and Northern Wildlife Research Centre, Wildlife Research Division, Environment and Climate Change Canada, Saskatoon, SK, Canada

Abstract

Foxes (*Vulpes* spp.) are small, solitary canids with relatively low social complexity compared to more gregarious canids, such as wolves and dogs. They are, therefore, expected to have a relatively simple vocal repertoire, with limited low-intensity sounds for close communication and many high-intensity sounds for long-distance communication. Arctic foxes (*Vulpes lagopus*), like many other foxes, are largely solitary outside of the breeding season. However, they have the largest litter size in the order Carnivora and may experience enhanced social complexity during the breeding season. In this study, we document the vocal repertoire of the Arctic fox during the breeding season, and how it changes before and after the emergence of pups. We also describe the relationship between vocalizations and other denning behaviours. Camera-traps captured six distinct sounds produced by breeding pairs of Arctic foxes and their young at dens: territorial barks, warning barks, alarm calls, cooing, whines and growling. Our study shows that although high-intensity sounds, such as territorial barks, are an important form of long-distance communication among Arctic foxes, low-intensity sounds and sound mixing are used on their dens following pup emergence. Thus, Arctic fox vocalization may be more complex than previously documented.

Keywords
Communication; canine; *Vulpes lagopus*; polar; barking; *Ursus arctos*

Correspondence
Kayla J. Buhler, Department of Forestry and Field Studies, Inland Norway University of Applied Sciences, 80 Anne Evenstads vei, NO-2480 Koppang, Norway.
E-mail: kayla.buhler@inn.no

Introduction

Arctic foxes (*Vulpes lagopus*) are the smallest canid in Arctic and Subarctic regions (Audet et al. 2002) and have a circumpolar distribution. They are well adapted to freezing temperatures, with thick fur found in two genetically distinct colour morphs: blue and white (Prestrud 1991). Arctic foxes are largely generalists and serve as both scavengers and predators in coastal and inland ecosystems. However, inland foxes are also specialist predators of lemmings and other native Arctic rodents that undergo cyclical population irruptions (Fuglei & Ims 2008). Arctic foxes adjust their reproductive output along with food limitation, with larger litter sizes during peaks in small rodent abundance (Strand et al. 1999; Meijer et al. 2013), which drives population increases in the following year (Samelius & Alisauskas 2017). Females are monoestrous and gestate for about 52 days before pups are born in late spring (Audet et al. 2002). Breeding pairs are predominantly monogamous, and there is significant paternal investment in pup rearing; however, extrapair paternity and dens with multiple attendant mothers have been documented (Cameron et al. 2011).

Though the non-vocal behaviour of Arctic foxes has been well studied (Audet et al. 2002), few publications have described their vocalizations (Cohen & Fox 1976; Ovsyanikov et al. 1988; Frommolt et al. 2003). Canids are thought to communicate by using a gradient and mixture of sounds that convey information, along with non-vocal body posturing, olfactory cues and facial expressions (Cohen & Fox 1976). Increased social complexity among Canidae, as seen with wolves (*Canis lupus*) and dogs (*C. familiaris*), corresponds with increased complexity of vocalizations, with more mixing of sounds, facial expressions and body postures (Fox 1975; Freeberg et al. 2012). This implies that foxes, which are largely solitary when compared to wolves and dogs, should have a less complex vocal repertoire during most of their annual cycle (Cohen & Fox 1976; Audet et al. 2002). In general, canids

Citation: *Polar Research* 2024, *43*, 9430, http://dx.doi.org/10.33265/polar.v43.9430

produce 12 basic vocalization types, including whines, yelps, yips, screams, barks, coughs, growls, coos, howls, mews, grunts and guttural 'clicks' (Cohen & Fox 1976). Vocalization in *Vulpes* spp. is thought to be distinct from other canids, with a higher incidence of cooing, guttural 'clicks' and screams (Cohen & Fox 1976).

Many of these vocalization studies were published prior to current technology that allows for video and audio sharing. Here, we document the vocal repertoire of Arctic foxes and relationships between vocalizations and other denning behaviours from video recordings obtained throughout the denning season at Karrak Lake, Nunavut, Canada. Specifically, the goal of this study was to document the vocal repertoire of foxes during the breeding season and examine whether it changed after the emergence of pups on dens.

Methods

Study area

At Karrak Lake (67°14′N, 100°15′W), adult foxes have been captured and marked in May for the past 20 years to monitor population dynamics (Samelius & Alisauskas 2017). This location in Arctic Canada hosts one of the largest goose colonies in the Circumpolar Arctic, which is home to roughly 90% of the world's population of Ross's geese (*Anser rossii*) and 15% of the world's population of lesser snow geese (*A. caerulescens caerulescens*) during the summer (Kerbes et al. 2006). Associated with the goose colony, a large population of Arctic foxes is supported by rodents and migratory geese during the breeding season (Samelius et al. 2011). Predators in the area include wolves, grizzly bears (*Ursus arctos*), wolverines (*Gulo gulo*) and golden eagles (*Aquila chrysaetos*).

Camera-trapping and video recording

Studies of infectious diseases and Arctic foxes have been conducted for over 10 years at Karrak Lake. Videos from dens were collected as a part of this larger study to verify the presence and number of fox pups at each site (Buhler et al. 2020; Buhler et al. 2022). Adult foxes captured for disease research were sedated and aged, sexed and tagged with colour-coded plastic tags on each ear for unique identification (Samelius et al. 2003). For this study, fox behaviour was monitored at all active dens in the study area (six dens before pup emergence and five dens after pup emergence) during the summers of 2019 and 2022. Dens and breeding pairs were not always the same between spring and summer, as multiple dens failed and/or moved; dens successfully filmed in spring may not have been included in the summer sampling, and new dens and breeding pairs found during summer may have been added.

Camera traps (Bushnell Brown Trophy Camera, model 119537) were placed at den sites with signs of current use, such as digging (to keep the den entrance open), tracks, fresh faeces and visual observation of foxes. Cameras were set to take videos for the longest length of time available (ranging from 5, 10 and 15 seconds, depending on the age of the camera), with a 3-second delay until the start of the next video. Camera-trap images and videos collected during 2–5 days (depending on the distance from our base camp) in late May to early June allowed us to determine the presence of females that had shown evidence of lactation during live-trapping in May or that had enlarged nipples and fur loss on the abdomen. Cameras were placed again at den sites in early to late June for 2–6 days to identify the number of pups at each site.

The videos from each camera were retrieved and reviewed, and sounds were assigned to six vocalization types—territorial barks, warning barks, alarm calls, cooing, whines and growling—on the basis of the description of canid sounds by Cohen & Fox (1976). Sound mixing was defined as the presence of two or more distinct sounds in one vocal sequence. Associations between the sound and other behaviour observations at dens were used to characterize the purpose of the sound (for example, alarm calls were associated with the presence of a predator or researcher). Several distinct communicative non-vocal behaviours were also documented, including tail wagging, teeth baring, ear flattening, eye squinting, crouching, bowing, pawing, stretching and jumping. Additional footage obtained by researchers during live-trapping of pups was also reviewed. Links to videos containing audio and visual examples are provided in Table 1. In this study, all observed dens were from monogamous breeding pairs.

Results and discussion

We obtained 111 minutes of video from six dens before pups emerged from the dens from late May to early June. Foxes were seen in 24% of these videos (27 minutes). Pups emerged from dens between early and late June, depending on when breeding had taken place. They were estimated to be between three and four weeks old based on their size, mobility and the presence of open eyes. We obtained 522 minutes of video from five dens after pups emerged from early to late June, in which pups and adults were seen in 55% of the videos (288 minutes). In addition to foxes, cameras were triggered by tall grass moving in the wind and other animals, including birds,

Citation: *Polar Research* 2024, *43*, 9430, http://dx.doi.org/10.33265/polar.v43.9430

caribou (*Rangifer tarandus*), predators and insects. A summary of the observations for each sampling session is available in Table 2.

Before pup emergence from dens, adult females and, to a lesser degree, males cleared out den entrances. Females and males were also seen scent-marking at den entrances, often after digging or exiting the den. This included urination, scooting of the hind end and rubbing the face (cheeks) and body in snow surrounding den entrances (Table 1). Both females and males used territorial barks and cooing on the den before pup emergence. Only females were seen whining on camera during this time. No growling or warning barks were observed on the den for each breeding pair before pups were seen on camera.

Territorial barking

Adult territorial barks are high-intensity vocalizations that carry long distances and are used to communicate with mates and competitors (Frommolt et al. 2003; Table 1, Fig. 2). Territorial barking was the most frequent vocalization that we documented at the dens before pup emergence and was often observed following digging, scent-marking and on entry or exit from the den. Barks are unique for each fox, allowing them to distinguish among members of their social group and to differentiate their own group from other groups (Frommolt et al. 2003). Interestingly, adult territorial barks were less frequent at dens following pup emergence, though they were still used when other foxes were nearby. Occasionally (observed on only 11 videos, 10 of which were from one den), pups displayed territorial barking after emergence. Pups were roughly 3–4 weeks of age when this behaviour was observed for the first time, immediately following emergence, which may reveal a crucial stage when pups begin to develop their own unique bark.

Whining and interactions between breeding pairs

Resident adult females and males often interacted on the den both before and after pups emerged. Body posture was consistent across all interactions. Females appeared submissive, with a crouched and lowered body, squinted eyes, pinned-back ears and an open mouth, emitting a shrill whining noise as males approached, with or without food (Fig. 1). Females also showed vigorous tail-wagging and licked the face of the male to encourage sharing of food when present. The male response varied among breeding pairs. Males made cooing/chittering noises and territorial barks in response to the female's sounds and non-vocal behaviours. Males displayed no submissive behaviour when approaching the den (Table 1). No evidence of regurgitation was documented, even after the emergence of pups. This has been listed as a common behaviour in a previous study by Strand et al. (2000), who described that 30% of begging sequences from pups resulted in females regurgitating food. This was documented in Norway, which may suggest that there are interesting behavioural differences between Scandinavian and North American Arctic fox populations. Differences between studies may also reflect differences in food abundance, leading to differences in the frequency of regurgitation.

Parental roles and male involvement at dens

Both males and females brought food back to the den, though only females ate at dens. Similarly, only females were seen resting and sleeping at dens during late spring before the emergence of pups, often for prolonged periods (seven hours in the instance of Den 3; Table 2). This likely occurred early post-partum when nursing pups required more frequent feedings (Audet et al. 2002). Male involvement varied at different dens as the summer progressed. At one site, the

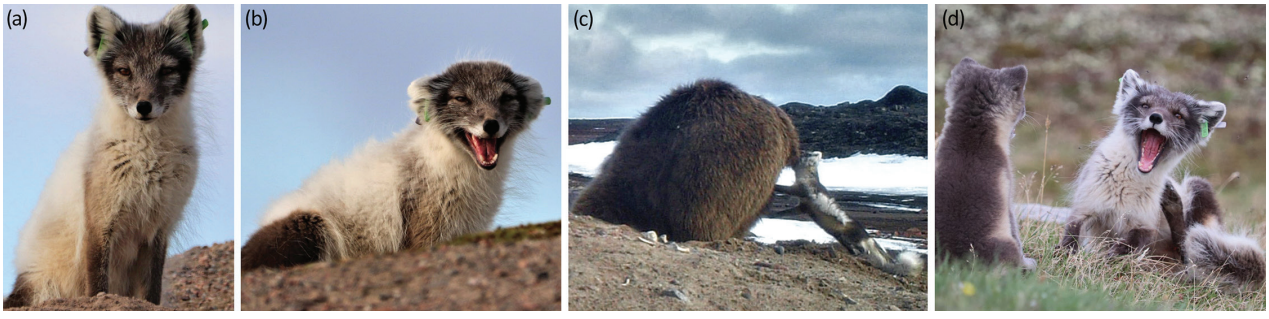

Fig. 1 Photographs illustrating some behaviours observed at Arctic fox dens. Female Arctic fox (a) before and (b) after the arrival of her mate, showing a crouched and lowered body with pinned-back ears and eye squinting. (c) Female fox biting a grizzly bear as it digs at the den. (d) Female fox baring teeth in response to harassment by a pup. (Figure created with BioRender.)

Table 1 Video examples of Arctic fox vocalizations and non-vocal communicative behaviours at dens.

Behaviour	Theorized purpose	Link to video
Vocal		
Territorial bark	Communicate presence over long distances; declaring ownership of an area and or item	https://www.youtube.com/watch?v=qj2RujG82gA&ab_channel=KaylaBuhler
Territorial bark by pups	May be practicing vocalization or seeking attention	https://www.youtube.com/watch?v=MoYQlab1ya8&ab_channel=KaylaBuhler
Whining by female fox	Females greeting males and begging for food, submissive behaviour, generally combined with tail wagging	https://www.youtube.com/watch?v=nIoACgUjGMI&ab_channel=KaylaBuhler
Cooing or chittering	Calling out pups from dens/affection	https://www.youtube.com/watch?v=OqzUCSDaxkE&ab_channel=KaylaBuhler https://www.youtube.com/watch?v=_zVF6pfDy80&ab_channel=KaylaBuhler
Warning bark	Express caution or to encourage pups to enter den	https://www.youtube.com/watch?v=VjcBbwpdw2o&ab_channel=KaylaBuhler
Whining by pups	Generally done while begging for food	https://www.youtube.com/watch?v=VzYJatVJB4I&ab_channel=KaylaBuhler
Growling by pups	Fighting between litter mates	https://www.youtube.com/watch?v=qBd1REN5fZY&ab_channel=KaylaBuhler
Alarm call	Express anxiety and fear; warn pups and drive predators away from dens	https://www.youtube.com/watch?v=eCDIl00ACBE&ab_channel=KaylaBuhler
Sound mixing	Mixing of different types of vocalizations that may be used to convey multiple messages	https://www.youtube.com/watch?v=6SBPSOoCWhI&ab_channel=KaylaBuhler
Non-vocal		
Scent marking	Individual identification and marking territory	https://www.youtube.com/watch?v=qXZUycYwHX4&ab_channel=KaylaBuhler
Open mouth/teeth baring	Warning signal used towards pups, especially after weaning	https://www.youtube.com/watch?v=cXrDxsUJKDY&ab_channel=KaylaBuhler

male was only seen at the den before pup emergence, and the female was the sole provider of food for the six pups. This male was not observed again during the rest of the study; it may have died, abandoned the den or provided support away from the den. At other dens, males were more engaged in the pup rearing—generally by bringing food to the den—but did not spend much time near the den or interacting with pups (Table 2). The male in an older breeding pair (both roughly six years old) at one den spent considerably more time resting and grooming on the den compared to other males (Den 6; Table 2). This male interacted with the pups but did not initiate any play behaviour. Thus, investment by males at dens appeared to vary individually and may depend on age, experience and abundance of food such as lemmings (*Lemmus* spp.) and voles, which often vary substantially between years (Samelius & Alisauskas 2017). Following weaning, which generally occurred when pups were between six and eight weeks of age, both males and females responded to apparent harassment by pups by holding their mouths open and pinning back their ears (Table 1, Fig. 1). This may be used to convey a message similar to snarling and teeth baring observed among other canids.

Cooing and interactions between parents and pups

The most common vocalization recorded at dens from breeding female foxes was cooing, a short and repeated low sound made without opening the mouth (Fig. 2). Females began cooing at dens before pups emerged in early June, likely to announce their presence to pups. Adult males cooed in response to adult females during greetings on the den, when entering den entrances before pup emergence, and while interacting with pups on the den. This vocalization was previously observed and documented as a low chittering sound that the mother emitted to encourage pups to exit the den (Audet et al. 2002). However, our recordings show that both parents coo frequently with their offspring outside of the den or when mates interact together. Cooing was often expressed by adult females to initiate grooming or nursing or to interrupt fighting among siblings. Pups often reciprocated this vocalization when interacting with their parents, particularly their mothers.

Citation: *Polar Research* 2024, *43*, 9430, http://dx.doi.org/10.33265/polar.v43.9430

Table 2 Summary of sampling effort, adult attendance at dens, predator visitation and number of vocalizations observed on videos before and after pups emerged from the dens.

Before pups emerged from dens[a]	Den						Total
	1	2	3	4	5	6	
Days camera was at the den	5	5	3	3	2	2	20
Video clips collected with foxes	28	72	42	38	7	3	190
Video clips with breeding female	23	20	35	18	4	3	103
Video clips with breeding male	3	55	9	19	3	0	89
Predator visits on the den	3	0	0	0	0	1	4
Vocalizations by adult foxes							
Video clips with alarm calls	1	0	0	0	0	0	1
Video clips with territorial barks	1	9	2	8	3	0	23
Video clips with whining	0	3	0	0	1	0	4
Video clips with cooing	0	4	3	1	0	0	8
After pups emerged from dens[b]	Den						Total
	7	8	9	10	11		
Days camera was at the den	5	3	6	2	2		18
Video clips collected with foxes	21	356	59	515	222		1173
Video clips with breeding female	18	347	37	351	178		931
Video clips with breeding male	1	16	12	0	10		39
Predator visits to the den	4	2	22	373	182		583
Vocalizations by adult foxes	1	0	1	1	0		3
Video clips with alarm calls							
Video clips with territorial barks	0	0	0	14	2		16
Video clips with whining	5	3	0	0	0		8
Video clips with cooing	0	8	1	0	0		9
Video clips with warning bark	1	19	0	113	20		153
Vocalizations by pups	0	0	0	2	19		21
Video clips with territorial barks							
Video clips with whining	1	0	0	10	0		11
Video clips with cooing	4	7	0	105	27		143
Video clips with warning bark	0	0	0	49	20		69

[a]Late May to early June. [b]Early June to late June.

Pup vocalizations and behaviour at dens: whining, growling and warning barks

In addition to cooing when interacting with adults, pups had a range of other vocalizations. The most common was a shrill whining noise similar to the sound that females made in response to their male mates returning to the den with food (Tables 1, 2). The posture of pups was not submissive during the early weeks following emergence from the den. However, as pups were weaned and began accepting solid food from parents, pinned-back ears, crouched/lowered body posture and tail wagging all became common when greeting adults on the den. Growling and vigorous tail-wagging were also observed when pups were competing for food, fighting or playing (Table 1). Play progressively increased at dens as pups became older, including playing with food or other inanimate objects (such as feathers, plants and rocks) and wrestling with siblings. Not all communication was vocal for young foxes, especially play-soliciting behaviour (tail wagging, teeth baring, jumping, bowing and pawing at siblings). Pups were also seen practicing skills like food-caching and stalking. No noises were detected from within the dens during the first weeks of June, when pups had yet to emerge from dens and were presumably <3 weeks of age (Audet et al. 2002). However, vocalizations increased as they spent more time outside of dens, and, in response to the presence of researchers, a warning bark was often detected from inside dens following pup emergence. Warning barks by adults and older pups appear to signal danger nearby and often encouraged pups to run back into the den. The warning bark was distinctly different from alarm calls (screams) by the adults, described in Fig. 2.

Alarm calls: screams

We often observed predators visiting dens, including wolves, wolverines, grizzly bears and golden eagles.

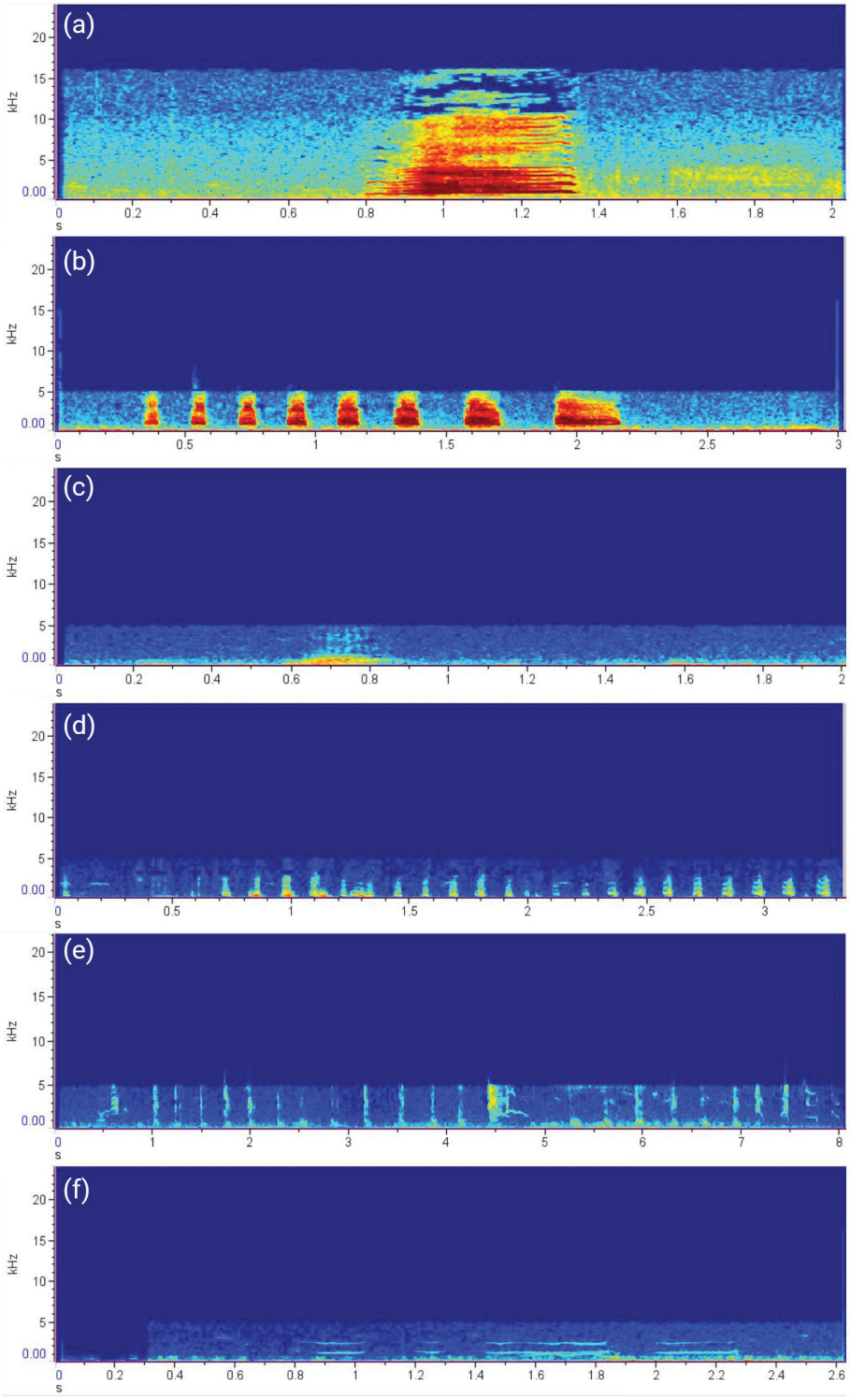

Fig. 2 Audio spectrograms of each vocalization depicting frequency (kHz) over time (seconds), including (a) an alarm call, (b) territorial bark, (c) warning bark, (d) cooing, (e) growling and (f) whining. (Audio was isolated from videos using the online video editing programme Biteable, and spectrograms were generated by Raven Lite 2 software from The Cornell Lab of Ornithology. (Figure created with BioRender.)

Citation: *Polar Research* 2024, *43*, 9430, http://dx.doi.org/10.33265/polar.v43.9430

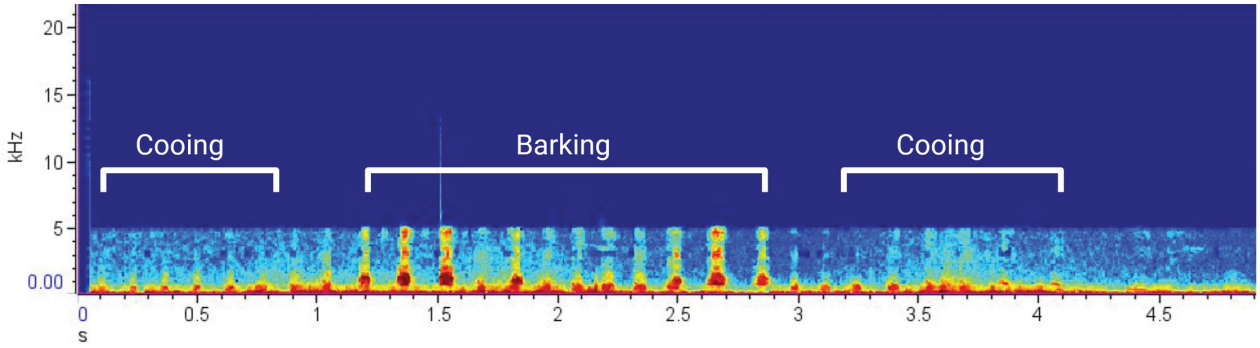

Fig. 3 Audio spectrogram depicting frequency (kHz) over time (seconds) for sound mixing from an adult female fox that includes both cooing and the territorial bark. Audio was isolated from videos using the online video editing programme Biteable, and spectrograms were generated by Raven Lite 2 software from The Cornell Lab of Ornithology. (Figure created with BioRender.)

Females present at dens during these visits vigorously attempted to drive the predator away from the den while emitting short and shrill alarm calls (referred to as 'contact screams' by Cohen & Fox [1976]), which were repeated every 2–3 seconds (Table 1). Female Arctic foxes were seen biting the hind end of wolverines and bears while they were digging at the dens (Fig. 1), as previously reported by Samelius et al. (2002) and Hendrickson et al. (2005) for the same fox population. In both of our recorded interactions lasting > 5 minutes, predators left the den with food previously cached by adult foxes. We did not observe any pup mortalities due to predation, though this has been reported from other Nearctic regions, such as Alaska (Garrott & Eberhardt 1982). Females often cached numerous food items around the den and moved these food items frequently between different den entrances, possibly to confuse predators intent on kleptoparasitizing potential food.

Concluding remarks

Since the complexity of canid vocalization is related to social complexity (Cohen & Fox 1976), and Arctic foxes are largely solitary outside of the breeding season, the vocal repertoire of this species was not expected to be very complex (Fox 1975; Cohen & Fox 1976; Audet et al. 2002). However, in this study, we identified a variety of high- and low-intensity sounds produced at various times throughout the breeding season, suggesting that the vocal repertoire of Arctic foxes may be more complex than previously known. We also observed mixing of different sounds (most commonly cooing and barking; Fig. 3), a level of vocal complexity that, to our knowledge, has not been previously described for Arctic foxes. The sound repertoire collected during the period following pup emergence confirms that the most common sounds used at dens were low-intensity vocalizations (cooing, whining, growling and warning barks), representative of strong social units and close-contact interactions (Cohen & Fox 1976). The use of high-intensity vocalizations (territorial barks and alarm calls) was typically observed from adult Arctic foxes for long-distance intraspecific communication and perhaps danger signalling along with anti-predator behaviour. Long-distance communication associated with territoriality became less frequent following pup emergence (Frommolt et al. 2003). Thus, the use of high-intensity and low-intensity vocalizations may vary for Arctic foxes, with lower intensity sounds becoming more common during periods of increased kin or familial interactions.

Acknowledgements

The authors thank Dana Kellett for preparing for the Karrak Lake field seasons and Robin Owsiacki and Sophie Adams for assistance in the field.

Disclosure statement

The authors report no conflict of interest.

Funding

Funding was provided by a Natural Sciences and Engineering Research Council of Canada Discovery and Northern Research Supplement, Polar Knowledge Canada, Weston Family Foundation and ArcticNet Network.

Ethics and approvals

Research was approved by the University of Saskatchewan Animal Research Ethics Board under the protocol

number 2010-0159, Nunavut Wildlife Research Permits for fox (2019-010, 2021-18), Aboriginal Affairs and Northern Development Canada Land Use Permit (N2018N0008), Nunavut Water Board (8BC-KAR1727), Environment and Climate Change Canada Permit to Conduct Scientific Research on Migratory Birds through SC-NR-2019-NU-003 and Migratory Bird Sanctuary Permit through MM-NR-2019-NU-008.

References

Audet A.M., Robbins C.B. & Larivière S. 2002. *Alopex lagopus*. *Mammalian Species 713*, 1–10, doi: 10.1644/1545-1410(2002)713<0001:AL>2.0.CO;2.

Buhler K., Bouchard É., Elmore S., Samelius G., Jackson J., Tomaselli M., Fenton H., Alisauskas R. & Jenkins E. 2022. Tularemia above the treeline: climate and rodent abundance influences exposure of a sentinel species, the Arctic fox (*Vulpes lagopus*), to *Francisella tularensis*. *Pathogens 12*, article no. 28, doi: 10.3390/pathogens12010028.

Buhler K., Maggi R.G., Gailius J., Galloway T.D., Chilton N.B., Alisauskas R.T., Samelius G., Bouchard É. & Jenkins E.J. 2020. Hopping species and borders: detection of *Bartonella* spp. in avian nest fleas and Arctic foxes from Nunavut, Canada. *Parasites & Vectors 13*, article no. 469, doi: 10.1186/s13071-020-04344-3.

Cameron C., Berteaux D. & Dufresne F. 2011. Spatial variation in food availability predicts extrapair paternity in the Arctic fox. *Behavioral Ecology 22*, 1364–1373, doi: 10.1093/beheco/arr158.

Cohen J.A. & Fox M.W. 1976. Vocalizations in wild canids and possible effects of domestication. *Behavioural Processes 1*, 77–92, doi: 10.1016/0376-6357(76)90008-5.

Fox M.W. 1975. Evolution of social behaviour in canids. In M.W. Fox (ed.): *The wild canids.* Pp. 429–459. New York, NY: Van Nostrand Reinhold and Company.

Freeberg T.M., Dunbar R.I. & Ord T.J. 2012. Social complexity as a proximate and ultimate factor in communicative complexity. *Philosophical Transactions of the Royal Society B: Biological Sciences 367*, 1785–1801, doi: 10.1098/rstb.2011.0213.

Frommolt K.H., Goltsman M. & Mcdonald D.W. 2003. Barking foxes, *Alopex lagopus*: field experiments in individual recognition in a territorial mammal. *Animal Behaviour 65*, 509–518, doi: 10.1006/anbe.2003.2064.

Fuglei E. & Ims R.A. 2008. Global warming and effects on the Arctic fox. *Science Progress 91*, 175–191, doi: 10.3184/003685008X327468.

Garrott R.A. & Eberhardt L.E. 1982. Mortality of Arctic fox pups in northern Alaska. *Journal of Mammalogy 63*, 173–174, doi: 10.2307/1380691.

Hendrickson C.J., Samelius G., Alisauskas R.T. & Larivière S. 2005. Simultaneous den use by Arctic foxes and wolves at a den site in Nunavut, Canada. *Arctic 58*, 418–420.

Kerbes R.H., Meeres K.M., Alisauskas R.T., Caswell F.D., Abraham K.F. & Ross R.K. 2006. *Surveys of nesting mid-continent lesser snow geese and Ross's geese in eastern and central Arctic Canada, 1997–98. Canadian Wildlife Service Technical Report Series 447*. Saskatoon, SK: Canadian Wildlife service, Prairie and Northern Region.

Meijer T., Elmhagen B., Eide N.E. & Angerbjörn A. 2013. Life history traits in a cyclic ecosystem: a field experiment on the Arctic fox. *Oecologia 173*, 439–447, doi: 10.1007/s00442-013-2641-8.

Ovsyanikov N.G., Rutovskaya M.V., Menyushina I.E. & Neprintseva E.S. 1988. Social behaviour of Arctic fox (*Alopex lagopus*): repertoire of sound reactions. *Zoologicheskii Zhurnal 67*, 1371–1380. (In Russian with English summary.)

Prestrud P. 1991. Adaptations by the Arctic fox (*Alopex lagopus*) to the polar winter. *Arctic 44*, 132–138.

Samelius G. & Alisauskas R.T. 2017. Components of population growth for Arctic foxes at a large Arctic goose colony: the relative contributions of adult survival and recruitment. *Polar Research 36*, article no. 6, doi: 10.1080/17518369.2017.1332948.

Samelius G., Alisauskas R.T. & Larivière S. 2011. Seasonal pulses of migratory prey and annual variation in small mammal abundance affect abundance and reproduction by Arctic foxes. *Polar Biology 34*, 1475–1484, doi: 10.1007/s00300-011-1005-2.

Samelius G., Alisauskas R.T., Larivière S., Bergman C., Hendrickson C.J., Phipps K. & Wood C. 2002. Foraging behaviours of wolverines at a large Arctic goose colony. *Arctic 55*, 148–150, doi: 10.14430/arctic699.

Samelius G., Lariviere S. & Alisauskas R.T. 2003. Immobilization of Arctic foxes with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®). *Wildlife Society Bulletin 31*, 192–196.

Strand O., Landa A., Linnell J.D., Zimmermann B. & Skogland T. 2000. Social organization and parental behavior in the Arctic fox. *Journal of Mammalogy 81*, 223–233, doi: 10.1644/1545-1542(2000)081<0223:SOAPBI>2.0.CO;2.

Strand O., Linnell J.D., Krogstad S. & Landa A. 1999. Dietary and reproductive responses of Arctic foxes to changes in small rodent abundance. *Arctic 52*, 272–278, doi: 10.14430/arctic932.