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RESEARCH ARTICLE

# Cranial features of mainland and Commander Islands (Russia) Arctic foxes (*Vulpes lagopus*) reflect their diverging foraging strategies

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**ABSTRACT**

Populations of Arctic fox (*Vulpes lagopus*) in the Commander Islands, in the Russian Bering Sea, have been isolated since the Pleistocene and differ substantially in their cranial features from their mainland counterpart. Small rodents, the main prey of mainland Arctic foxes, are not found in the Commander Islands, where the main food source for Arctic foxes are large sea birds and marine mammals. Here we assessed whether differences in foraging strategy, particularly the size of available prey, could explain the observed differences in cranial features between mainland and island Arctic foxes. Because a large gape is necessary when foraging on large prey, we compared gape angles between islands and mainland in a sample of dry crania. We found an enlarged gape angle in both island populations. We also compared the rostrum to cranium length ratio and found it to be similar for the mainland and Bering Island Arctic foxes; however, a rostrum contraction was found in the Mednyi Island Arctic foxes. We show that cranial differences between mainland and Commander Islands fox populations could be explained by their different foraging ecology. Furthermore, the relative rostrum contraction in the Mednyi Island foxes provides further evidence for cranial resistance to deformation during biting. These results show the importance that distinct foraging strategies can have in Arctic fox divergent evolution, and, consequently, on future conservation plans for the two Commander Islands subspecies.

**KEYWORDS**

Carnivores; island isolation; cranial morphology; divergent evolution; prey size; conservation

**ABBREVIATIONS**

ANOVA: analysis of variance; CBL: overall condylobasal length; RL: absolute rostrum length

## Introduction

Populations of Arctic fox, *Vulpes lagopus*, living on the two Commander Islands (Fig. 1a) located 200 km off the eastern coast of the Kamchatka Peninsula, in the ice-free part of the Bering Sea, have been isolated from mainland Arctic foxes for about 10 000 years (Goltsman et al. 1996; Goltsman et al. 2005; Geffen et al. 2007; Džikija 2008). Because of their phenotypic differences, the island populations have been classified as different subspecies of Arctic fox: *V. l. semenovi* Ognev (1931) on Mednyi Island and *V. l. beringensis* Merriam, 1902, on Bering Island. Arctic foxes living on the mainland (*V. l. lagopus* Linnaeus, 1758) migrate extensively and effectively constitute a single mainland population (Dalén et al. 2005).

These three subspecific populations of Arctic foxes have evolved separately since they first diverged, and the literature confirms numerous morphological differences between Arctic foxes in the Commander Islands and those on the mainland (Calkin 1944; Zagrebelnyj & Puzacenko 2006; Nanova 2009; Nanova 2010). Both island subspecies are significantly larger than their mainland conspecific: the average winter body mass of Arctic foxes in the Commander Islands is 5–7 kg for males and 4.5–6 kg for females, while on the mainland it is 3.2–4.5 kg for males and 3.0–3.5 kg for females (Goltsman et al. 2005). The Commander Islands foxes have a more robust cranium: it is longer and wider at the carnassials and zygomatic arches, and has more developed crests (Nanova 2009).

It has been observed that the food sources available to Arctic foxes living in the Commander Islands are different from those available to the mainland population (Angerbjörn et al. 1999; Anthony et al. 2000; Zagrebelnyj 2000a; Goltsman et al. 2010). Small rodents, such as lemmings of the genera *Lemmus* and *Dicrostonyx* and voles of the genera *Microtus*, *Clethrionomys* and *Arvicola*, are the main prey of Arctic foxes on the mainland throughout the year (Angerbjörn et al. 1999; Anthony et al. 2000; Eide et al. 2004). Rodents are absent on Mednyi Island, and even though the northern red-backed vole (*Clethrionomys rutilus*) had been introduced on Bering Island by the end of the 19th century, it plays a minor role in the diet of Arctic foxes on that island (Zagrebelnyj 2000b).

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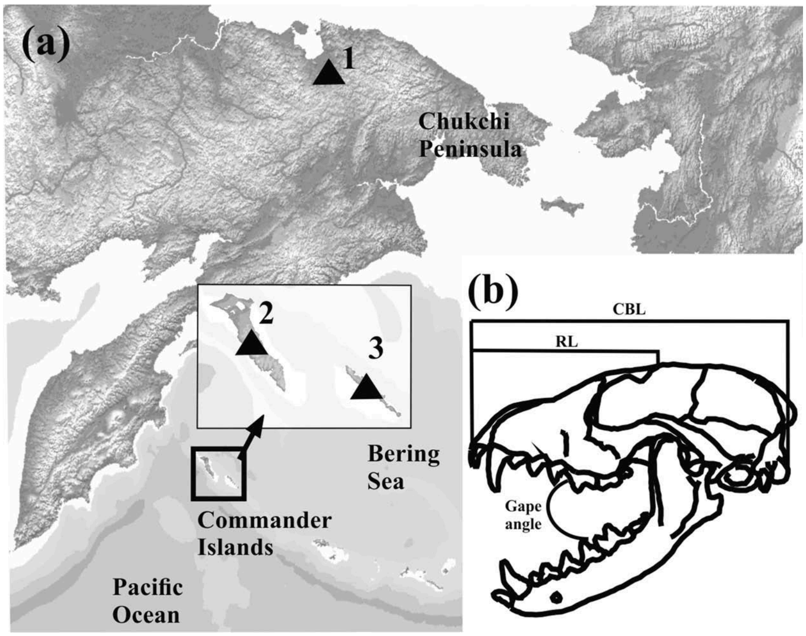

**Figure 1.** (a) Map showing the location where the mainland (approximate coordinates 68°26'N, 171°39'E) specimens was collected (1), and the location of the two Commander Islands, (2) Bering Island (approximate coordinates 55°4'N, 166°4'E) and (3) Mednyi Island (approximate coordinates 54°40'N, 167°50'E); the copyright-free map was downloaded from www.maps-for-free.com and modified. (b) Lateral view of an Arctic fox cranium showing the three measurements taken in this study, CBL, RL and gape angle.

The main summer food sources for Arctic foxes on both Commander Islands are seabirds, especially the large northern fulmar (*Fulmarus glacialis*), which form great rookeries on the islands and can amount to about 90% of the diet of Arctic foxes (Goltsman et al. 2010). Storm-petrels, puffins and guillemots are also consumed (Zagrebelnyj 2000b; Goltsman et al. 2010). Before the drastic population decline in 1975–1977, as a result of an outbreak of mange, Arctic foxes on Mednyi Island used the rookeries of the northern fur seal (*Callorhinus ursinus*) as food sources, preying on newborn pups, carcasses and placentas (Celnokov 1970; Naumov et al. 1981). Such foraging behaviour can still be observed among Arctic foxes on Bering Island (Zagrebelnyj 2000a).

In winter, when preferred prey is scarce, island Arctic foxes forage primarily on carcasses of marine mammals, generally of the sea otter (*Enhydra lutris*; Zagrebelnyj 2000a; Goltsman et al. 2010). Some foxes on the mainland follow polar bears (*Ursus maritimus*), foraging on what remains from their prey (Bannikov 1970). In contrast, there are no large predators in the Commander Islands that can cut open the carcasses of marine mammals and effectively prepare them for Arctic fox consumption (Marakov 1964). Yet, marine mammals or their carcasses have constituted a significant portion of the diet of Arctic foxes in the recent past (Barabaš-Nikiforov 1937; Barabaš-Nikiforov 1939; Ilina 1950; Celnokov 1970; Smirin et al. 1979; Zagrebelnyj 2000a,b; Goltsman et al. 2010).

Food items available to Commander Islands foxes are generally larger than those usually available to mainland foxes. With a wingspan of 102–112 cm and weighing 450–1000 g, the size of the northern fulmar is comparable to that of an adult fox (Sudilovskaja 1951). In some parts of the mainland, Arctic foxes also forage on large birds, such as geese (Celnokov 1970; Naumov et al. 1981), during the nesting season, but this behaviour is limited by the availability of such prey. Because foraging on such large prey requires a large gape (Slater & Valkenburgh, 2009; Figueirido et al. 2011; Santana 2016), it is expected that Arctic fox populations in the Commander Islands have a larger gape, as well as an elongated rostrum to enlarge the gape arc length, when compared to mainland Arctic foxes.

In this paper we assess whether differences in foraging strategy, particularly the size of available prey, explain the observed differences in cranial features between mainland and Commander Islands Arctic foxes. We measured the length of the cranium, the length of the rostrum and the jaw gape angle in a sample of Arctic foxes from the three geographically isolated populations to test the hypothesis that Arctic foxes that forage on large prey have evolved a wider jaw gape angle than foxes which do not. Although there is no evidence for differences in feeding behaviour between sexes, we also tested for sexual dimorphic differences in cranium and rostrum length and gape.

## Material and methods

We measured to an accuracy of 1 mm CBL, RL and gape angle on dry crania of adult Arctic foxes (Fig. 1b) collected (1) on the Chukchi Peninsula on the mainland (43 specimens; 22 males and 21 females), (2) on Bering Island (41 specimens; 21 males and 20 females), and (3) on Mednyi Island (30 specimens; 18 males and 12 females). The crania used for this study are housed in the Zoological Museum of M.V. Lomonosov Moscow State University. The raw measurements are provided as supplementary material.

The two linear measurements, CBL and RL, were assessed with a Sylvac digital calliper. To test the stated hypothesis, CBL and RL were compared among the three populations. Then, to compare rostrum proportions among populations, the residuals of a linear regression of RL on CBL were compared. To measure the maximal gape, each cranium was fixed rigidly, and the mandible was attached at the maximal estimated gape, as indicated by the fit of the craniomandibular joint. During this procedure the condyle was prevented from slipping away from the cotyle, so that a space would not be created between them. The angle between the cranium and the mandible at the craniomandibular joint was measured with a protractor. Gape angle was then compared among populations. An ANOVA was performed for each pair of populations, for each measurement. The same analyses were performed between males and females to compare sexual dimorphism among populations.

## Results

CBL is similar for Bering Island (mean ± standard deviation, 128.68 ± 4.92) and Mednyi Island (127.65 ± 4.82) foxes, while the CBL of mainland foxes (121.30 ± 4.18) is smaller in comparison with either island populations (Table 1). When comparing the absolute RL in a population-level sample we found that Bering Island foxes (77.32 ± 3.44) have larger absolute RL in comparison to both mainland foxes (74.12 ± 1.97) and Mednyi Island foxes (74.93 ± 3.81). At the same time, the absolute RL is significantly different between Mednyi Island foxes and mainland foxes.

We found that the rostrum of Mednyi foxes is relatively shorter in comparison to both Bering Island and mainland foxes (Table 1, RL/CBL). The rostrum proportions do not differ between Bering Island and mainland foxes.

The maximal gape angle of mainland foxes (50.72 ± 5.42) is significantly smaller (Table 1) than the gape angle of either island Arctic foxes. However, gape angle does not differ significantly between Mednyi Island foxes (60.70 ± 6.23) and Bering Island foxes (57.12 ± 7.43).

Males have a longer cranium and rostrum than females in all three populations, but there are no differences in rostrum proportions between the sexes. Likewise, we found no differences in gape angle between males and females (Table 2).

## Discussion

The absence of differences in cranium and rostrum length and gape angle between males and females in any of the three Arctic fox populations shows that sexual dimorphism does not affect our interpretation of interpopulation differences. Even if males have longer crania and rostra in comparison to females, which agrees with previously reported data showing that male Arctic foxes are larger than females (Ognev 1931; Zagrebelnyj 2000b; Nanova 2009), rostrum proportions between males and females remain constant among all three studied populations.

As known from previous publications (Calkin 1944; Vibe 1967; Goltsman et al. 2005; Zagrebelnyj & Puzacenko 2006; Nanova 2009; Nanova 2010), body size and cranial size are significantly larger in island populations of Arctic foxes than in the mainland one. However, we did not find significant elongation of the rostrum relative to the rest of the cranium in island foxes. On the contrary, the rostrum

Table 1. ANOVA for CBL, RL, residuals of linear RL/CBL regression, and gape angle between populations: mainland (main), Mednyi Island (Med) and Bering Island (Ber). Significant values are in boldface.

| | | CBL | | RL | | RL/CBL | | Gape angle | |
|---|---|---|---|---|---|---|---|---|---|
| Population pairs | df | F | *p* | F | *p* | F | *p* | F | *p* |
| Main/Med | 1 | **35.26** | **<0.0001** | **7.72** | **<0.01**[a] | **12.23** | **<0.01**c | **52.96** | **<0.0001** |
| Main/Ber | 1 | **53.16** | **<0.0001** | **45.13** | **<0.0001** | 0.00 | 1.000000 | **20.48** | **<0.0001** |
| Med/Ber | 1 | 0.67 | 0.41587 | **7.68** | **<0.01**b | **9.89** | **<0.01**d | 4.59 | 0.035690 |

[a] $p = 0.006983$. [b] $p = 0.007170$. [c] $p = 0.000815$. [d] $p = 0.002452$.

Table 2. ANOVA for CBL, RL, residuals of linear RL/CBL regression and gape angle between males (m) and females (f) in each population: mainland (main), Mednyi Island (Med) and Bering Island (Ber). Significant values are in boldface.

| | | CBL | | RL | | RL/CBL | | Gape angle | |
|---|---|---|---|---|---|---|---|---|---|
| Populations | df | F | *p* | F | *p* | F | *p* | F | *p* |
| m/f main | 1 | **51.20** | **<0.0001** | **27.13** | **<0.0001** | 2.62 | 0.113193 | 3.01 | 0.090265 |
| m/f Ber | 1 | **34.72** | **<0.0001** | **14.98** | **<0.001**[a] | 0.43 | 0.515839 | 0.31 | 0.580861 |
| m/f Med | 1 | **29.17** | **<0.0001** | **13.02** | **<0.01**b | 0.10 | 0.754175 | 0.19 | 0.666259 |

[a] $p = 0.000403$. [b] $p = 0.001188$.

of Mednyi Island foxes is found to be relatively shorter in comparison to both mainland and Bering Island foxes. The rostrum of Bering Island foxes is absolutely (but not relatively) longer than in mainland foxes. This result means that the proportion of rostrum to cranial length for Bering Island foxes is similar to that of mainland foxes. At the same time, the proportion of rostrum and cranial length is significantly different for Mednyi Island foxes in comparison to the two other studied subspecies.

As for gape angle, we found that mainland Arctic foxes have a significantly smaller gape than Commander Islands foxes. These differences in gape angle between mainland and island populations seem to reflect their foraging strategies. We know that mainland Arctic foxes forage primarily on small rodents, while seabirds and marine mammals, which significantly match or exceed Arctic foxes in weight and size, are the only prey available to Commander Islands foxes. Therefore, a wider gape angle seems to be an adaptive requirement and we suggest that large prey was an important selective agent responsible for the observed morphological differences in the cranium between the mainland population and the Commander Islands populations.

However, it has been shown that for foraging on larger prey a larger bite force is demanded (Wroe et al. 2005; Christiansen & Wroe 2007), while gape angle has a negative effect on bite force (Herring & Herring 1974; Greaves 1982; Fields et al. 1986; Dummont & Herrel 2003; Bourke et al. 2008). We interpret the relative rostrum contraction of Mednyi Arctic fox as necessary to keep the bite force large at a larger gape angle. A shorter rostrum shifts bites proximally, and bite force is markedly affected by the point of contact along the dental row. Our results concur with others (Ognev 1931; Calkin 1944; Zagrebelnyj 2000b; Nanova 2009) in showing that the overall cranial size enlargement of both subspecies of Commander Islands Arctic foxes is necessary when foraging on larger prey to increase both gape arc length and bite force. Further investigations should improve our understanding of the relationship between cranial features and the size of prey of Arctic fox populations in the Commander Islands.

## Conclusion

Differences in cranial features between mainland and Commander Islands Arctic foxes can be explained by their diverging foraging strategies. We found a wider gape angle in both island populations, which is consistent with a large prey diet. A rostrum contraction in the Mednyi Island Arctic foxes can also be explained by their foraging on large prey, providing further evidence for cranial resistance to deformation during biting in the Arctic fox population of that island (Nanova et al. In press). These results show the importance that distinct foraging strategies can have in Arctic fox divergent evolution, and, consequently, on future conservation plans for the two Commander Islands subspecies.

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## Disclosure statement

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