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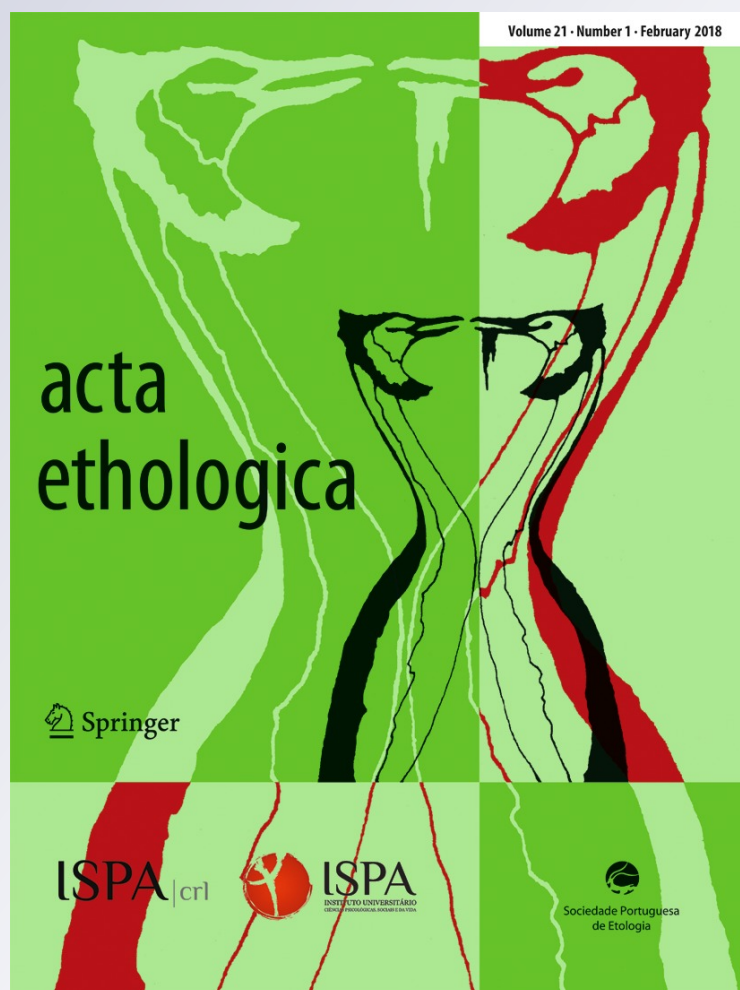
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Agonistic behavior between introduced beaver (*Castor canadensis*) and endemic culpeo fox (*Pseudalopex culpaeus lycoides*) in Tierra del Fuego Island and implications

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Abstract Over the last 70 years, introduced beavers (*Castor canadensis*) have been successful in establishing and modifying the landscape of southernmost Patagonia. Habitat availability and lack of large carnivorous predators have contributed to this success. The Fuegian culpeo fox (*Pseudalopex culpaeus lycoides*) is an endangered subspecies and the largest native predator found in Tierra del Fuego Island. The predatory behavior of a culpeo towards a beaver was studied by analyzing a video footage recovered by tourists, and consumption of beaver was documented with camera traps. An ethogram of the predatory behavior sequence was developed and true durations and percentage of time allocated to each behavior were analyzed. The “capture” and “watch”

behaviors had the highest durations within the predatory sequence (61.83 and 42.61 s, respectively), while “rest” was the most frequent maintenance behavior observed (93.82 s). The culpeo may provide the only natural population control for beavers, although up to date, there is no evidence to confirm this ecological role. Based upon photos from camera traps, we confirm the occurrence of fox feeding on beavers. This is the first description of the stages of the interaction between a Fuegian culpeo fox and a North American beaver under natural conditions. We discuss the ecological implications of this interaction.

Keywords Conservation implications · Culpeo attack · Endangered fox · Invasive species · Patagonia · Predatory behavior

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Introduction

Invasive species are those able to establish and reach high densities or large distributions from few introduced individuals (Davis and Thomson 2000; Kolar and Lodge 2001). They have been recognized as the second most important cause of biodiversity loss in the world and the first on insular ecosystems (Courchamp et al. 2003; Mack et al. 2000). IUCN Red List corresponds in recognizing invasive species as one of the most important threats to native biodiversity, costing 5% of the global economy (Burgiel and Muir 2010). In this regard, animal invaders can cause extinction of vulnerable native species through predation, competition, and habitat alteration (Mack et al. 2000) and also through transmission of potential pathogens and emergence of diseases (Daszak 2000; Harvell et al. 2002; Smith et al. 2006; Smith et al. 2009; Dunn and Hatcher 2015).

One of the most conspicuous invaders, causing major habitat transformation in Patagonia, is the North American beaver (*Castor canadensis*). This beaver was intentionally introduced by the Argentinean government in Tierra del Fuego Island during 1946, when 20 individuals from Canada were released in the northeastern shore of Fagnano Lake, along with a hunting ban, which lasted until 1981 (Lizarralde 1993; Pietrek and Fasola 2014). Currently, it is estimated that the invasive population of beavers would be in the order of 80,000 individuals (Lizarralde 1993; Jaksic et al. 2002; Skewes et al. 2006) having spread from Tierra del Fuego Island to neighbor islands such as Hoste, Navarino, Lenox, Picton, Nueva, and Dawson (Lizarralde 1993; Jaksic et al. 2002; Anderson et al. 2006; Skewes et al. 2006), and even reaching the continent (Skewes et al. 2006). Beavers are considered ecosystem engineers (Jones et al. 1997; Wallem et al. 2007), and their impacts include changes in habitat structure, nutrient cycling and soil properties, modifying food webs through competition, and even favoring other invasive species (Valenzuela et al. 2014; Crego et al. 2016). Recently, it has been estimated that between 2005 and 2014, in the northern part of Argentinean Tierra del Fuego, beaver ponds have increased by 85% (Pietrek and González-Roglich 2015) and the extent of this habitat modification may be affecting terrestrial local native or endemic species.

Inundation provides amphibious beavers with a refuge from predators which, in its native range, include wolves (*Canis lupus*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), black bears (*Ursus americanus*), river otters (*Lutra canadensis*), and cougars (*Puma concolor*), among others (Collen and Gibson 2000; Hartman 1994). From these predators, wolves have been described as the only species that regularly prey on beavers, having the potential to control its populations in North America (Shelton and Peterson 1983).

Long periods of glaciation led to isolation of Tierra del Fuego, which has resulted in low diversity (Humphrey and Péfaur 1979) and high endemism (e.g., 22% of mammals are endemic; Glade 1993). Three large (> 1 kg) native mammals of Tierra del Fuego are the endemic Fuegian culpeo fox (*Pseudalopex culpaeus lycoides*), the guanaco (*Lama guanicoe*), and the southern river otter (*Lontra provocax*), the latter preferring coastal environments (Gomez et al. 2010).

Up to date, there are no reports on native Fuegian fauna preying on beavers (Lizarralde 1993; Lizarralde et al. 2004) and diet studies conducted in Tierra del Fuego have not reported beaver consumption by native carnivores (Atalah et al. 1980; Jaksic et al. 1983; Jaksic and Yáñez 1983). Field reports by governmental officials in Navarino Island describe fang's scars in beavers, possibly inflicted by feral dogs or culpeo foxes (Wallem et al. 2007), although the latter have not been reported in Navarino Island (Markham 1971).

The Fuegian culpeo fox is one of the six subspecies of culpeo distributed exclusively in the Tierra del Fuego archipelago, now considered endangered (Cabrera 1931; Osgood 1943;

Glade 1993). Its habitat in Tierra del Fuego and neighboring islands is mainly southern beeches forest (Markham 1971). The Fuegian culpeo is the largest of the subspecies (Gomez et al. 2010), and probably due to energetic requirements (Wang et al. 2004), it has a hyper-carnivorous diet (Jaksic and Yáñez 1983; Wayne et al. 1989). Recently, Novaro et al. (2009) described that *P. culpaeus lycoides* (weighing up to 14 kg; C Briceño unpublished data; $n = 15$) hunt and prey on guanacos, which can be ten times bigger than them; thus, culpeos could potentially predate on smaller preys such as beavers.

In the present manuscript, we describe the agonistic interaction between a Fuegian culpeo fox and an introduced beaver, filmed by tourists in Tierra del Fuego National Park, Argentina. We discuss conservation implications of this new mammalian interaction in light of future beaver management.

Materials and methods

Study area

Tierra del Fuego Island (54° 00'S, 70° 00'W) is the largest island in South America, with an area of 47,992 km², and is located south of the Strait of Magellan, separated by 4 km at the closest point from the mainland. The southern portion of the island is dominated by the Andes mountain range where peaks reach 2000 masl, and flattens to a plateau towards the north (Dalziel 1981). Monthly mean temperatures vary between −4 °C in winter and 10 °C in summer, and mean annual precipitation is 500 mm, with frequent snowfall during autumn and winter (Tuhkanen et al. 1999). Politically, the island is divided in two, being Chilean on the western half and Argentinean on the eastern half.

Visual material and video analyses

Predatory behavior by a Fuegian fox on a beaver was filmed during a tourism excursion in the winter (July) of 2007 at “La Bajada del Turbal” (54° 50' 30"S, 68° 30' 58"W), inside the Tierra del Fuego National Park, Argentina. Film footage was later delivered to a park ranger.

The footage has an extension of 4 min and 43 s (Electronic Supplementary Material). The behavior of the culpeo and beaver was described and organized into an ethogram modified from MacNulty et al. (2007) (Table 1). Once the ethogram was developed, continuous recording was applied to determine true durations (in seconds) and sequence of behavioral components involved in the predatory pattern using the Observer XT 2011 (Noldus software, version 11, Noldus Information Technology, The Netherlands). The beavers' behavior was described, but not quantified.

Two additional videos retrieved from a camera trap (Bushnell® Trophy Cam™ HD Essential Trail Camera)

Table 1 Ethogram of the recorded behaviors performed by the fox

Behavior	Definition
Predatory behavior sequence	
Watch	Fixating on beaver while not traveling (e.g., standing, sitting, or crouching).
Approach	Fixating on and traveling towards the beaver.
Attack individual	Running after or lunging at the beaver.
Capture	Biting and restraining beaver by the neck, tail or other part of the body.
Maintenance behaviors	
Walk	Moves forward from point A to B in a four-beat gait.
Rest	Lying down with eyes closed or open.

placed at Aserradero Vicuña at Karukinka Natural Park (54° 08' 03"S, 68° 43' 01"W) in Chilean Tierra del Fuego on 7th of March 2015 were included (Figs. 2 and 3). The camera trap was set up next to a beaver carcass, which is a usual practice done by the park rangers in order to monitor this invasive rodent within the protected area.

Results

After the first revision of the video footage, the constructed ethogram included four behaviors associated to the predatory behavior sequence of the culpeo and two maintenance behaviors described in Table 1. True durations (seconds) and percentage of time allocated to each behavior are presented in Table 2. From the predatory sequence, “capture” comprised the highest percentage of time followed by “watch” while, within the maintenance behaviors, “rest” had the highest duration.

The sequence analysis and true durations of the behaviors involved in the predatory behavior are presented in Fig. 1. From the four behaviors, “capture” and “watch” involved the highest amount of time of the sequence.

The beaver was observed to deploy two behaviors during the footage. These were “galloping” on dry land (locomotor

behavior) and “seeking protection in water” (protection behavior).

Additionally, images retrieved from camera traps show culpeo consuming beaver's carcasses. In Fig. 2, a group of Fuegian culpeos (potentially a female and two offspring) is observed at night ingesting beaver meat from a specimen that was caught by a trap. In the second image (Fig. 3), an adult culpeo fox is observed scavenging on a trapped beaver carcass during the day. These photographs are provided to demonstrate that foxes can and will eat beaver's meat when provided the opportunity.

Discussion

The present manuscript describes for the first time an agonistic interaction between a Fuegian fox and a beaver, involving a predatory sequence with no predation. This interaction occurred during the southern winter; when food is scarce and thus, it may represent an opportunistic event on which the fox sought resources during the cold season.

MacNulty et al. (2007) established an ethogram for carnivore predatory behavior based upon wolves (*Canis lupus*). We were able to identify in the fox four of the six behavioral components proposed by MacNulty et al. (2007) (Table 1 and Fig. 1). The behavior “search” may not have been identified in the culpeo due to the opportunistic nature of the film, so we cannot conclude it is not present. The “attack group” component is not present because only one beaver was observed. The fox spent most of its time resting after the beaver escaped, which occurs towards the end of the footage after the failed attack (35%; Table 2). During the last seconds, the fox pants intensely, probably due to fatigue as result of the predatory behavior displayed.

One key aspect to the outcome of the observed footage is the presence of a creek where the beaver can seek refuge. Beavers are known to remain close to watercourses as means of security. In addition, due to their size (up to 45 kg), beavers are known to be strong enough to drown a dog or a wolf, by pulling them underwater (Gorbunova et al. 2008). The beaver displayed two behaviors associated with protection against predation: “galloping” and “seeking of protection in the water.” According to Patenaude (1984), seeking protection in water is a reaction to disturbance that appears at the age of 6–10 days in beavers. Galloping behavior has also been described as an escape reaction on dry land (Patenaude 1984). The beaver's behavioral reactions were successful in this case, likely due to the presence of a nearby stream.

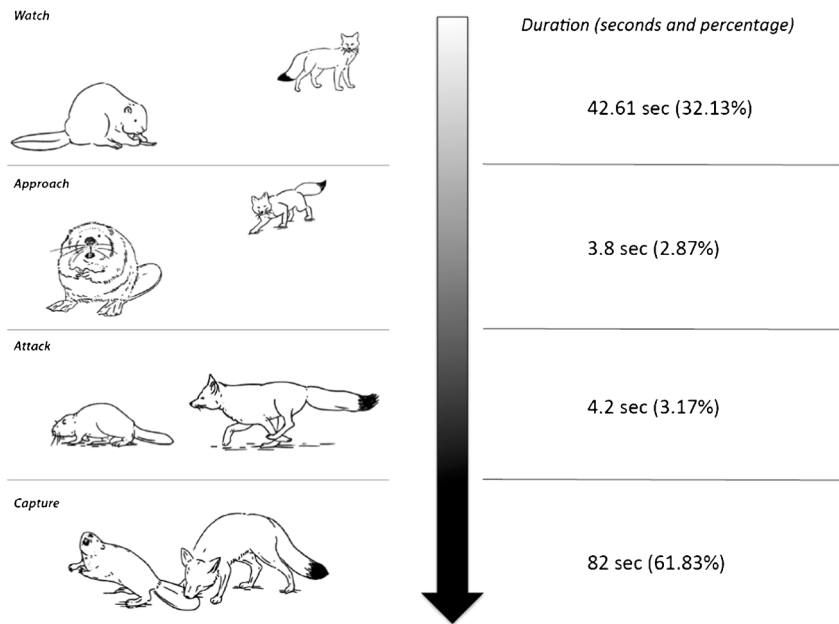
Conclusions

Culpeos are known to display predatory behavior towards juvenile guanacos (Novaro et al. 2009) and attack huemul

Table 2 True durations (seconds) and percentage of time allocated to the behaviors studied

Behavior	True duration (s)	Percentage of time
Watch	42.6	16.0
Approach	3.8	1.4
Attack-ind.	4.2	1.6
Capture	82.0	30.9
Walk away	39.3	14.8
Rest	93.8	35.3
Total	265.8	100.0

Fig. 1 Illustration describing the sequence of the predatory behavior of a culpeo attacking a beaver. True duration and percentage of time allocated to each behavior within the predatory sequence are included



deer (*Hippocamelus bisulcus*), both fawns (Corti et al. 2010) and sick adults (Briceño et al. 2013); all of which are heavier than culpeos. Based upon the behaviors towards a beaver analyzed in this study, we conclude that culpeos can also deploy predatory behavior towards beavers, even including them in their diet when possible. Whether this predatory interaction results in actual predation will probably depend on age and health status of beaver attacked and on proximity to streams where beavers can seek refuge.

Implications

The Fuegian culpeo is the largest native terrestrial carnivore in Tierra del Fuego Island and, as such, may play a role on limiting some populations of introduced mammal species, which outnumber native species in this area by almost two

to one (Valenzuela et al. 2014). Culpeos can consume large numbers of introduced mammals where these become abundant and in some cases even base the bulk of their diets on them (Jaksic et al. 1983; Novaro et al. 2000). The culpeo's limiting effect on beaver populations would depend to some extent on the ability of this predator to switch among different prey, both introduced and native, as their numbers change in space and time, as has been shown for other canids (Letnic et al. 2012; Randa et al. 2009). In any case, our study suggests that a new and possibly strong interaction may have appeared in Tierra del Fuego involving culpeos and beavers as a source of food as prey or carrion, and perhaps even facilitating an interaction with other introduced prey, such as muskrats (Crego et al. 2016; Appendix).

We believe that three aspects of the reported interaction need to be considered due to their implications for management:

First, given the current distribution and abundance of beavers, the culpeo could have better predatory chances on these populations in suboptimal beaver habitats and in areas through



Fig. 2 A group of Fuegian foxes scavenging over a trapped beaver carcass in Tierra del Fuego

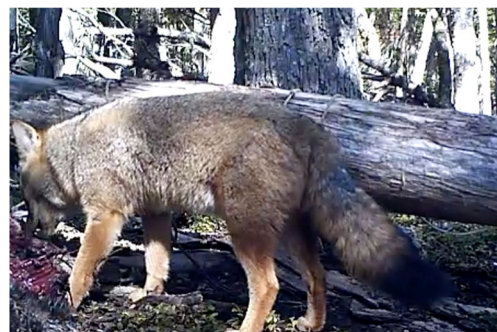


Fig. 3 An adult Fuegian fox scavenges over a trapped beaver carcass in Tierra del Fuego

which beaver are likely to disperse, where their vulnerability to predation may increase. Mainly, these would be streams with shallow watercourses and areas away from streams. Furthermore, dispersing juveniles, smaller and perhaps with less defensive skills, would likely be more vulnerable to predation than adults.

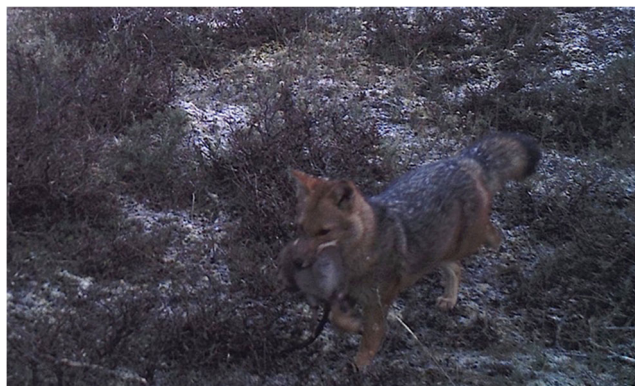
Second, in Tierra del Fuego, there is currently an important removal effort to control beaver populations through trapping. Traps are being deployed and revised sporadically and often beaver carcasses consumed by foxes. It is unknown how this availability of carcasses may be subsidizing culpeo fox populations or other introduced canids such as chilla foxes (*Pseudalopex griseus*) or dogs. The latter increasing in importance, with feral dog populations reported becoming abundant at the Argentinean side of the Island (Schiavini and Narbaiza 2015).

Finally, this newly observed interspecific interaction may have an impact on the health of Patagonic ecosystems as these close encounters and interactions could augment cross species transmission of pathogens, which in turn have the potential to contribute to local wildlife extinctions (Daszak 2000; Harvell et al. 2002; Smith et al. 2006; Smith et al. 2009).

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Appendix

An adult Fuegian fox trots with a full adult muskrat in its muzzle, probably recently caught. Taken on a camera trap on the 28th of May of 2017 in Tierra del Fuego Island (54° 12' 12"S, 68° 77' 18"W)



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