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ORIGINAL ARTICLE

Canine distemper virus as a threat to wild tigers in Russia and across their range

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Abstract

Canine distemper virus (CDV) has recently been identified in populations of wild tigers in Russia and India. Tiger populations are generally too small to maintain CDV for long periods, but are at risk of infections arising from more abundant susceptible hosts that constitute a reservoir of infection. Because CDV is an additive mortality factor, it could represent a significant threat to small, isolated tiger populations. In Russia, CDV was associated with the deaths of tigers in 2004 and 2010, and was coincident with a localized decline of tigers in Sikhote-Alin Biosphere Zapovednik (from 25 tigers in 2008 to 9 in 2012). Habitat continuity with surrounding areas likely played an important role in promoting an ongoing recovery. We recommend steps be taken to assess the presence and the impact of CDV in all tiger range states, but should not detract focus away from the primary threats to tigers, which include habitat loss and fragmentation, poaching and retaliatory killing. Research priorities include: (i) recognition and diagnosis of clinical cases of CDV in tigers when they occur; and (ii) collection of baseline data on the health of wild tigers. CDV infection of individual tigers need not imply a conservation threat, and modeling should complement disease surveillance and targeted research to assess the potential impact to tiger populations across the range of ecosystems, population densities and climate extremes occupied by tigers. Describing the role of domestic and wild carnivores as contributors to a local CDV reservoir is an important precursor to considering control measures.

Key words: canine distemper virus, conservation threat, extinction, *Panthera tigris altaica*, population decline

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INTRODUCTION

Global populations of tigers, *Panthera tigris* (Linnaeus, 1758), are at an all time low, with numbers of reproductive females in the wild dropping below 1000 individuals (Walston *et al*. 2010). Pressure from agriculture, industry and urbanization has fragmented tiger habitat, such that remaining populations occupy less than 7% of their former range and more than half of the world's tigers are confined to habitat islands containing 25 or fewer individuals (Sanderson *et al*. 2006; Walston *et al*. 2010). Even in suitable habitat, tigers face a variety of threats, including competition with humans for prey resources, direct poaching to meet the demand for their body parts and retaliation due to conflicts with humans (Walston *et al*. 2010; Chundawat *et al*. 2011). While these anthropogenic factors are the main drivers of declining tiger numbers (Robinson *et al*. 2015), these depleted populations face new pressures associated with stochastic processes that have the potential to drive small, isolated populations to extinction. While inbreeding depression is well recognized as a threat to small populations (Kenney *et al*. 2014), disease agents (pathogens) can also be important drivers of stochastic extinction in carnivore populations (Thorne & Williams 1988; Timm *et al*. 2009); however, their potential impact on free-ranging tigers has received little research attention. In Russia, canine distemper virus (CDV) has recently been recognized as a cause of death in Amur tigers, *Panthera tigris altaica* Temminck, 1844 (Quigley *et al*. 2010; Seimon *et al*. 2013), and could pose a potential extinction threat, particularly to small populations (Gilbert *et al*. 2014). Recent reports have also confirmed cases of CDV in wild tigers in India, indicating that the threat may extend to tigers in other regions as well (ProMED 2014). The objectives of the present paper are: first, to assess our current understanding of the status and impact of CDV on Amur tigers; second, to consider the potential impact of CDV to tigers across their range; and third, to outline steps needed to assess and monitor the threat of CDV to tiger populations both in Russia and elsewhere across their range.

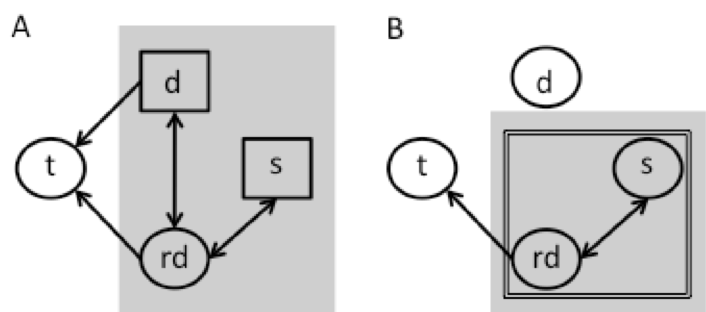
BIOLOGY OF CANINE DISTEMPER VIRUS

Canine distemper is caused by a paramyxovirus with a single-stranded RNA genome within the Morbillivirus genus, which has a near worldwide distribution (Williams 2001; Green & Appel 2006). Transmission of CDV primarily occurs through the respiratory tract during close contact with an infected individual, but quantities of the virus are also shed in the urine and feces. The virus generally enters the body via the respiratory tract by infecting alveolar macrophages, and then spreads rapidly throughout the lymphatic system (Ludlow *et al*. 2014). Infection of lymphatic cells, particularly T and B lymphocytes, and the severity of the resulting immunosuppression dictates the outcome of the disease (Green & Appel 2006). By the second week of infection the virus spreads to epithelial cells, resulting in respiratory and gastrointestinal signs as well as viral shedding in the urine (Ludlow *et al*. 2014). The virus also enters the brain by crossing the blood–brain barrier, or migrating along the olfactory nerve (Ludlow *et al*. 2014). Many animals die during the initial stages of the disease, but a proportion of the survivors may relapse some time later, with a progression of neurological signs (including behavioral changes, muscle twitching and seizures) as replication continues in the brain. Dogs may continue to shed the virus for up to 60 days (Green & Appel 2006), but captive tigers have been reported to shed the virus in urine for at least 150 days (V. Keahey 2014, pers. comm.), although this was based on the results of molecular testing (reverse transcription polymerase chain reaction [RT-PCR]), and therefore the presence of viable virus cannot be confirmed. Pathological lesions consistent with CDV infection were still present in a captive tiger with progressive neurological disease 18 months after initial exposure (Blythe *et al*. 1983), and may be analogous to 'old dog syndrome' described in domestic dogs (Green & Appel 2006).

Most families within the order Carnivora are susceptible to CDV infection (Deem *et al*. 2000). However, the severity of clinical disease varies widely, being largely subclinical in some species (e.g. in domestic cats), while causing severe systemic disease leading to high mortality in others (e.g. ferrets) (Williams 2001). Clinical infections and mortality have been recorded in a number of felids, but to date all published reports have been within the genera of *Panthera* (including lion, tiger, leopard, *Panthera pardus*, *s*now leopard, *Panthera uncia*, and jaguar, *Panthera onca* [Appel *et al*. 1994]) and *Lynx* (including Canadian lynx, *Lynx canadensis*, Iberian lynx, *Lynx pardinus*, and bobcat, *Lynx rufus*) (Daoust *et al*. 2009; Meli *et al*. 2010). Antibodies to CDV without clinical disease or mortality have been reported in a number of other cat species (including puma, *Puma concolor*, cheetah, *Acinonyx jubatus*, Geoffroy's cat, *Leopardus geoffroyi*, and ocelot, *Leopardus pardalis* [Biek *et al*. 2002; Munson *et al*. 2004; Fiorello *et al*. 2007; Dales Nava *et al*. 2008; Thalwitzer *et al*. 2010; Uhart *et al*. 2012]), suggesting that susceptibility may vary within the Felidae. This is supported by the low competence of domestic cats as CDV hosts during experimental studies (Appel *et al.* 1974), and relates to differences in the structure of the cellular receptor (CD-150 or signaling lymphocyte activation molecule [SLAM]) used by CDV to enter lymphoid cells (Ohishi *et al*. 2014). Clinical infections and mortality have also been recorded in other taxa, including rodents (Origgi *et al*. 2013), nonhuman primates (Yoshikawa *et al*. 1989; Sun *et al*. 2010) and peccaries (Appel *et al*. 1991).

The multi-host nature of CDV represents a particular threat to endangered populations in situations where they coexist with more abundant susceptible hosts, which can act as a reservoir of infection (see Fig. 1). The fortunes of many single-host pathogens are density-dependent, where a decline in host density (e.g. through infection-related mortality) leads to a reduced

Taken in isolation, populations of endangered species, such as tigers, are generally too small and at too low a density to maintain canine distemper virus (CDV) in the long term. These populations fall below a critical community size (CCS), beneath which a pathogen is unable to persist due to a depletion of susceptible hosts over time (Bartlett 1960). Multi-host pathogens, such as CDV, may represent a persistent threat to small populations, through regular spillover transmission from a pathogen reservoir. In the face of such complexity, a framework proposed by Haydon *et al*. (2002) for describing the constituents of a reservoir system provides a useful basis for understanding its functional dynamics. This defines a reservoir as one or more epidemiologically connected populations in which the pathogen can be permanently maintained and from which infection is transmitted to the defined target species (e.g. tigers). Individual populations that exceed the CCS, and can, therefore, maintain infection indefinitely are termed maintenance populations, although several non-maintenance populations could act synergistically to form a maintenance community. Finally, a source population is that which transmits infection directly to the target, and may either be a maintenance population, or be connected to the maintenance population as a transmission link to the target.
The structure and constituent populations within a CDV reservoir are likely to vary across the global tiger range depending on the diversity, density and demography of susceptible host species. In Russia, reservoir candidates include domestic dogs and abundant wild carnivores, including sable (*Martes zibellina*), red fox (*Vulpes vulpes*), raccoon dog (*Canis lupus familiaris*) and Eurasian badger (*Meles meles*). Two simplistic representations of possible reservoir structures in Russia are illustrated in diagrams A and B.



Populations can either be maintenance populations (squares) or non-maintenance populations (circles). Transmission of CDV occurs in the direction indicated by the arrows. In A, dogs (d) and sable (s) exceed the CCS and are maintenance populations, while only raccoon dogs (rd) and dogs act as source populations of CDV infection for tigers (t). In this case all 3 populations contribute to the reservoir (indicated in grey), and control measures would need to target both transmission from dogs and raccoon dogs to tigers. In B, no individual population exceeds the CCS, but transmission between raccoon dogs and sable is such that the 2 populations can form a maintenance community (represented by the black frame). In this case raccoon dogs represent the only source of infection for tigers, and control measures would need to target either one or both of the populations contributing to the maintenance community, +/or the transmission of virus from raccoon dogs to tigers. Clearly, these are just examples, and many other possible combinations exist. However, successful control of CDV requires management of infection in maintenance populations or communities and/or their transmission linkages with the tiger population.

Figure 1 Defining the canine distemper virus reservoir.

opportunity for infection. By contrast, more cosmopolitan multi-host pathogens may continue to infect rare host species in areas where a reservoir continues to act as a source of the virus, even as the endangered population declines. Outbreaks of CDV have been implicated in population declines and near extinction of several wildlife species, including the African wild dog, *Lycaon pictus* (Fanshawe *et al*. 1991), the Santa Catalina Island fox, *Urocyon littoralis catalinae* (Timm *et al*. 2009), and the black-footed ferret, *Mustela nigripes* (Thorne & Williams 1988).

Even in susceptible species, the epidemiology of CDV can be complex. For instance, CDV has been implicated in local population declines of lions and African wild dog in several areas in East Africa (Fanshawe *et al*. 1991; Roelke-Parker *et al*. 1996). However, in southern Africa, populations of these species have remained stable, despite high levels of CDV exposure (Alexander *et al*. 2010). Alexander *et al.* propose that habitat heterogeneity in southern regions led to a more complex host population structure, limiting the spread of outbreaks and enabling recolonization from surrounding areas in the wake of local extinctions. However, even in the more homogeneous grassland environments of East Africa, CDV-induced losses are not inevitable, with multiple waves of CDV exposure evident in the serology profiles of the lion populations without coincident sickness or population impact (Munson *et al*. 2008; Viana *et al.* 2015). Overt outbreaks among the lions of Serengeti in 1994 and Ngorogoro in 2001 were attributed to climatic patterns resulting in high vector numbers, with mortality from CDV associated with *Babesia* infection loads (Munson *et al*. 2008). The involvement of viral co-infections has been implicated in other cases of CDV mortality (Fix *et al*. 1989; Burtscher & Url 2007; Origgi *et al*. 2013), and, therefore, it is important to consider these, or other physiological stressors as a precursor to disease. In spite of this, apparently uncomplicated CDV infections have led to mortality in captive tigers in North America, Europe and Asia, and so it appears that clinical outcome is not always dependent on co-infections (Appel *et al*. 1994; Nagao *et al*. 2012; Seimon *et al*. 2013). This may be due to variation in the virulence of different CDV strains, although it should be noted that genetically diverse strains have caused mortality in *Panthera* species without apparent co-infections (including viruses from the Arctic-like, North America-2 and Asia-1 clades) (Appel *et al*. 1994; Nagao *et al*. 2012; Seimon *et al*. 2013).

CANINE DISTEMPER VIRUS IN AMUR TIGERS

Comparatively more is known about the health of wild tigers in Russia than any other range country, as samples are routinely collected whenever live or dead tigers are handled. Serum collected from tigers immobilized during the placement of telemetry collars and in response to tiger–human conflict situations provides a baseline for assessing pathogen exposure (Goodrich *et al*. 2012; Naydenko *et al*. 2012). No CDV antibodies were detected in 27 tigers sampled from 1992 to 1999, suggesting that tigers at this time were not exposed to the virus (Goodrich *et al*. 2012). However, Goodrich *et al*. (2012) report antibodies to CDV in 6 of 13 tigers captured between 2000 and 2004, suggesting the introduction of CDV into this population during the early 2000s. In November 2003, a tigress captured in the village of Pokrovka, Khabarovskii Krai (46.69°N, 134.03°E) was taken into care but died five weeks later (Quigley *et al*. 2010). Although ambulatory at the time of capture, this tigress was non-responsive to stimuli and unafraid of humans. She was later confirmed as the first case of CDV in a wild tiger (Seimon *et al*. 2013).

Further cases of CDV in Amur tigers were confirmed in 2010. These included a 3–4-year-old male captured near the village of Aleksayevka, Primorskii Krai (43.56°N, 132.00°E) during February 2010, and an 8.5-year-old tigress who entered the village of Ternei, Primorskii Krai (45.04°N, 136.78°E) and was shot on 1 June 2010 (Seimon *et al*. 2013). A third case in 2010 has recently been confirmed based on sequences obtained from archived tissues and involved an adult male tiger that was shot close to Ternei in January 2010 (Gilbert *et al.* 2014, unpubl. data). All of these animals displayed neurological signs and were unafraid of humans. Video footage of a tiger behaving in this characteristic manner was taken along the Vladivostok-Khabarovsk highway between the towns of Vyazemski and Bikin, Khabarovskii Krai during the spring of 2010 (http://tinyurl.com/las2yt7). Although this animal later died in care, no samples were available for analysis; therefore, CDV could not be confirmed in this case.

CANINE DISTEMPER VIRUS IN SIKHOTE-ALIN BIOSPHERE ZAPOVEDNIK

One of the most closely monitored populations of Amur tigers inhabits the Sikhote Alin Biosphere Zapovednik (SABZ) in Primorskii Krai. The reserve is of sufficient size to hold territories for 11 breeding females (assuming a territory of 384 km^2, with average overlap of 11% between adjacent female territories) and 4 breeding males (assuming a territory of 1160 km^2, with average overlap of 14% between adjacent male territories), and lies within a wider matrix of suitable habitat that enables tigers to disperse to and from surrounding areas. This protected area limits access, allowing only rangers and researchers, such that tigers in core areas may rarely, if ever, encounter humans. However, four villages (inhabited by between 67 and 5350 people in 2010) and a small number of isolated dwellings lie outside the protected area and represent a source of contact for tigers with territories along the reserve boundary, as well as individuals without territories that may move more widely through the landscape.

One of the confirmed CDV cases in 2010, the 8.5-year-old tigress known as T02 (referred to as Pt 2010-3 in Seimon *et al*. 2013), held a territory along the southern border of SABZ (Figs 2a and 3). This tigress had been captured in 2002 and 2005 as part of a telemetry study, yet no CDV antibodies were detected from routine samples. She was subsequently recaptured on 24 March 2010, by which time CDV antibodies were circulating (with a virus neutralization titre of 1:256 measured at the Washington Animal Disease Diagnostic Laboratory, Pullman, WA, USA). In view of subsequent events, and the strong protective immunity that develops in animals that survive infection, it is likely that T02 was already infected by March 2010.

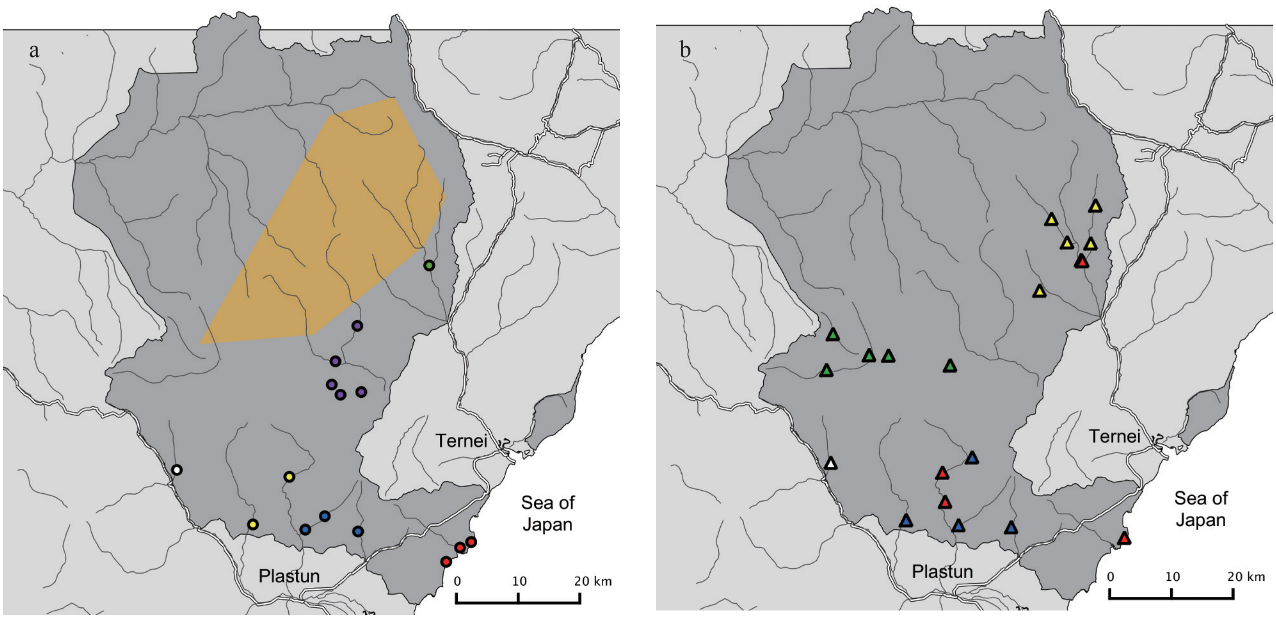


Figure 2 (a) Locations of resident female tigers in Sikhote-Alin Biosphere Zapovednik (dark grey). Map includes rivers (black lines) and roads (double lines). Tigresses are illustrated by circles, and include T02 (red), T5 (blue), T6 (yellow), T7 (green), T14 (purple) and T21 (white). Locations refer to camera trap captures made during 2009 and 2010, with the exception of T14, where captures from 2007 and 2008 are used (as this tiger was not photographed in 2009 or 2010). The home range of a further tigress (T47) is represented using a minimum convex polygon (orange), based on telemetry positions obtained during November and December 2009. (b) Locations of resident male tigers in Sikhote-Alin Biosphere Zapovednik (dark grey). The map includes rivers (black lines) and roads (double lines). Tigers are illustrated by triangles, and include T10 (green), T15 (yellow), T16 (red), T19 (white) and T27 (blue). Locations refer to camera trap captures made during 2009 and 2010, with the exception of T10, T15 and T19, where captures from 2007 and 2008 are used (as these tigers were not photographed in 2009 or 2010).

Tiger ID number	Estimated year of birth	Sex	Status	Date of last record	2006	2007	2008	2009	2010	2011	2012	Outcome
T02	2001	F	R	1 June 2010								Mortality (CDV confirmed)
T03	~1992	F	R	2007								Mortality (poached)
T04	~1998	M	R	2007								Mortality (poached)
T05	2001	F	R	27 October 2009								Mortality (unexplained)†
T06	2004	F	R	1 November 2009								Disappeared (unexplained)
T07	UNK	F	R	6 November 2009								Disappeared (unexplained)
T08	2006	F	DC	2008								Dispersed to North SABZ
T09/PT85	UNK	M	R	6 December 2007								Mortality (unexplained)
T10	UNK	M	R	2007								Disappeared (unexplained)
T14	UNK	F	R	Alive 2013								Alive (circa 2013)
T15	UNK	M	R	2007								Disappeared (unexplained)
T16/PT90	~1999	M	R	January 2010								Mortality (CDV confirmed)
T17/PT80	2005	F	R	16 November 2007								Mortality (poached)
T18/PT89	2006	M	DC	30 July 2008	*							Disappeared (dispersed?)
T19	UNK	M	R	February 2011	>							Mortality (natural)‡
T20	2006	F	DC	8 December 2008	*							Disappeared (dispersed?)
T21	UNK	F	R	13 April 2011		>						Disappeared (unexplained)
T25/PT88	2006	M	DC	22 September 2008	*							Emigrated from SABZ
T26/PT35	1993	F	R	2007								Disappeared (unexplained)§
T27	UNK	M	R	Alive 2013			>					Alive (circa 2013)
T29/PT96	2008	M	DC	17 January 2010			*					Disappeared (dispersed?)
T05 Cub A	2008	UNK	DC	2009			*					Disappeared (unexplained)
T05 Cub B	2008	UNK	DC	2009			*					Disappeared (unexplained)
T47/PT97	2008	F	R	11 December 2009			*					Mortality (unexplained)†
T30	UNK	M	R	Alive 2013					>			Alive (circa 2013)
T32/PT100	2006/07	M	R	December 2011				>				Mortality (poached)
T02 Cub A	2010	F	DC	May 2010				*				Mortality (CDV related)
T02 Cub B	2010	F	DC	May 2010				*				Mortality (CDV related)
T02 Cub C	2010	F	DC	May 2010				*				Mortality (CDV related)
T33	2010/11	F	DC	December 2011					*			Disappeared (dispersed?)
T34	2010/11	M	DC	December 2011					*			Disappeared (dispersed?)
T21 Cub A	2010	UNK	DC	2011					*			Mortality (natural)¶
T21 Cub B	2010	UNK	DC	2011					*			Mortality (natural)¶
T35/PT114	2009	F	R	Alive 2013					>			Alive (circa 2013)
T35 Cub A	2012	UNK	DC	Alive 2013							*	Alive (circa 2013)
T35 Cub B	2012	UNK	DC	Alive 2013							*	Alive (circa 2013)
T35 Cub C	2012	UNK	DC	Alive 2013							*	Alive (circa 2013)
PT95	2004	M	UNK	8 November 2009			>					Disappeared (dispersed?)††

Figure 3 A summary of camera trap captures of tigers in the central and southern regions of Sikhote Alin Biosphere Zapovednik (SABZ) between 2006 and 2013. Details of individual tigers include identity code, estimated year of birth, sex (F = female, M = male, UNK = unknown), status (R = resident, DC = dependent cub), the date and circumstances of last sightings. Identifiers with the prefix T refers to tigers recorded by camera trap, and the prefix PT refers to tigers fitted with radio collars. Both systems are used here to facilitate comparison with other publications. Transient tigers (recorded in only a single year) are excluded, as outcome could not be determined. Annual status of each tiger is indicated for animals captured at least once (dark green), not captured and presumed absent (yellow), not captured but subsequently confirmed (light green), or not surveyed for (grey). The timing of births are indicated by blue asterisks, and confirmed tiger deaths are indicated by cells outlined in red. Additional notes on the circumstances of tiger deaths and disappearances are provided as footnotes. The arrival of immigrants is indicated using blue arrows. (†Scavenged/predated by large carnivore. ‡Killed by another tiger. §Likely old age [14 years]. ¶Killed by T19. ††Possible transient. CDV, canine distemper virus.

Antibodies to CDV appear after 10 to 20 days post-infection in dogs (Green & Appel 2006), which if comparable in tigers would suggest an infection lasting at least 80 to 90 days in this tigress. By 1 May, T02 localized her movements, and (as was later confirmed) gave birth to a litter of three cubs. Although T02 had proven to be a typically attentive mother when raising her three prior litters, on this occasion her behavior was unusual, leaving the den for several days at a time before finally abandoning her cubs entirely on 17 May. She was subsequently observed at a nearby military outpost, before entering Ternei, where she was shot on 1 June 2010 to prevent injury to local residents. The presence of CDV was confirmed in brain tissue collected from T02, by sequencing of amplified gene products, and demonstration of consistent pathology (Seimon *et al* 2013). All three of her cubs consequently died. Evidence of CDV was not found in samples collected from 1 of those cubs, although decomposition may have hampered test sensitivity.

A recent re-examination of tissues collected from another SABZ tiger, T16 (referred to as Pt 2010-1 in Seimon *et al.* 2013) has confirmed that he was infected with CDV at the time of death (Gilbert *et al.* 2014, unpubl. data, Fig. 3). This tiger was an 11-year-old male, who occupied a territory that encompassed that of T02. On 31 December 2009, T16 approached and killed a local fisherman close to a group of houses 10 km west of Ternei. In common with other CDV cases, T16 displayed an unusual lack of fear, remaining in the open until he was shot and killed the following day. T16 was recorded in association with T02 in the fall of 2009. Assuming that T16 had sired the litter of T02, then mating must have occurred just a few days prior to his death (given a gestation period of 98–111 days [Wack 2003]). In captive tigers mortality from CDV usually occurs within days or weeks of developing clinical signs (Gould & Fenner 1983; Appel *et al*. 1994; Konjevic *et al*. 2011; Nagao *et al*. 2012; V. Keahey, pers. comm.), but the length of the refractive period (before clinical disease is evident) remains unknown, and a delayed onset may be possible (Blythe *et al*. 1983). Therefore, it is conceivable that T02 contracted her infection through contact with T16.

The deaths of T16, T02 and her 3 cubs coincided with a period of heavy losses for the SABZ tiger population (Fig. 3). Population estimates for the whole of SABZ based on snow tracking data indicated a decline from 25 tigers in 2008 to 9 by 2012 (Fig. 4). Camera trap surveys carried out in the central and southern sections of SABZ provide a more detailed account of the numbers and movements of a subset of the reserve's tigers, and highlight a similar decline (Fig. 3 [Soutyrina *et al*. 2013]). The population of 15 tigers identified on camera traps in 2008 (representing a minimum population) had declined to 7 identified by the start of 2011 (Table 1). Determining the cause of death in cryptic spe-

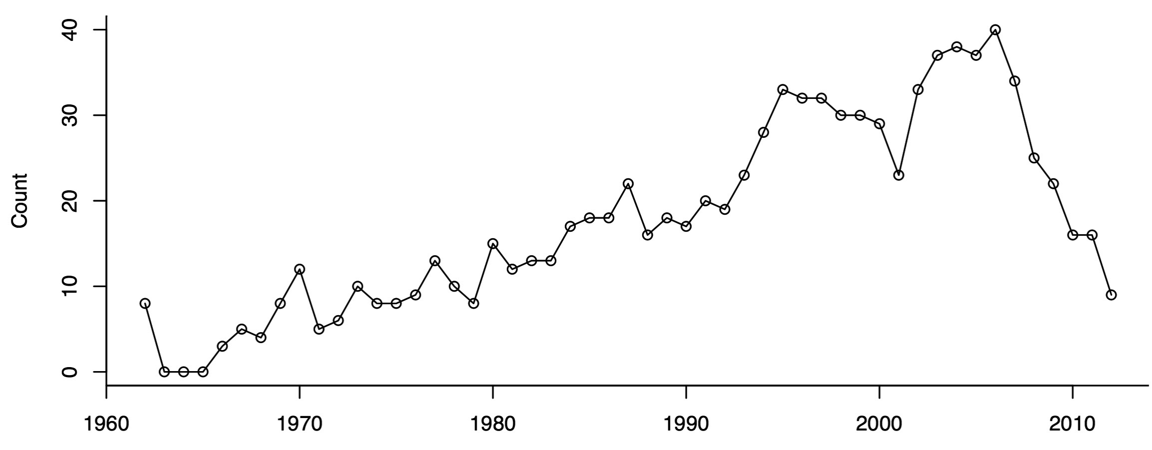


Figure 4 Annual tiger population estimates based on snow track surveys of Sikhote-Alin Biosphere Zapovednik from 1962 to 2012. Surveys are conducted annually from December through February along transects throughout the entire reserve.

Table 1 Population demographics of tigers in Sikhote-Alin Biosphere Zapovednik based on camera trapping surveys of central and southern regions of the reserve during 2006–2013. Numbers represent minimum estimates based on individual identifications of all tigers captured during camera trap surveys

Year	Tigers at year start (minimum)	Immigrants	Births	Deaths	Disappear	Emigrants	Transient
2006	?	0	1	?	?	?	4
2007	14	1	3	3	0	0	0
2008	15	2	2	2	3–5	2	0
2009	10–12[†]	1	2	3	0–2	0	1
2010	10	1	5	6	3	0	0
2011	7	2	2	3	0	0	1
2012	8	1	3	1	3	0	1
2013	8	4	8	?	?	?	0

"Deaths" refers to confirmed mortalities (e.g. where a body was recovered, or intelligence indicated a poaching incident), "Disappear" indicates absence of tigers where cause is unknown. [†]Two tigers (T10 and T15) disappeared some time during the years 2008 and 2009. However, no camera traps were set within their territories during this period to confirm the timing of their disappearance. For this reason a range of values is used to express the minimum number of tigers present at the start of 2009.

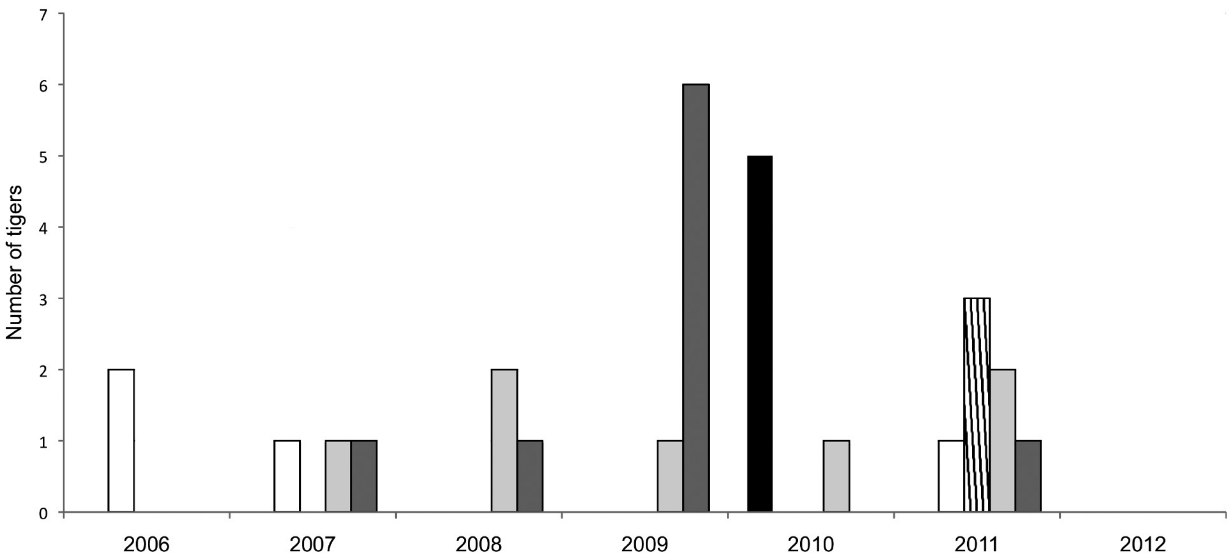


Figure 5 Annual tiger mortality and disappearances in Sikhote-Alin Biosphere Zapovednik between 2006 and 2012 attributed to poaching (white), canine distemper virus (CDV)-related (black), dispersal (confirmed or suspected based on disappearance at an age appropriate for dispersal [light gray]), natural (confirmed mortalities unrelated to humans and excluding CDV-related [cross hatch] and unexplained [dark grey]).

cies like tigers can be challenging, particularly in remote areas such as SABZ. However, the unexplained death or disappearance of 6 tigers during 2009 was unusual (Fig. 5), and it is possible that several of these may have been related to CDV infections that were undetected.

During late 2009 a resident adult tigress (T05, Fig. 3) was found dead, with no sign of her litter of 2 or more dependent cubs (although at approximately 1.5 years of age these tigers may have dispersed beyond the study area). The body of a second younger tigress (T47) was found several months later (Fig. 3). Both of these carcasses had been eaten by a bear or other large carnivore, although it was unclear whether this was the result of predation or scavenging. Consequently, the cause of death in these cases is open to speculation, and it is likely that a young newly independent tigress such as T47 could have succumbed to any of a number of possible dangers. However, T05 shared a territory with T16, the likely father of her cubs (Fig. 2), as did another resident adult tigress (T07) that was last recorded by camera trap on 6 November 2009 (Figs 2 and 3). A neighboring tigress (T06) also disappeared in late 2009, with the last camera trap record on 1 November 2009 (Fig. 3). Mortalities unrelated to CDV continued in early 2011, with the death of 2 dependent cubs attributed to infanticide carried out by an adult male (T19), who also succumbed soon after to injuries sustained in a fight with another tiger (Fig. 3). In May 2011, the carcass of a female with enlarged nipples (which suggested she was still nursing a litter) was found with 2 bullet wounds (This tiger was not captured or recorded on camera traps, and so is not included in Table 1).

These results suggest that there were multiple causes of death occurring in the SABZ population within a small (18-month) timeframe (late 2009–early 2011) (Fig. 3). CDV was not solely responsible for the dramatic declines in SABZ tigers during 2009 and 2010, but in a worse case scenario (including the unknown causes that might have been disease-related) it is possible that as many as 6 adults/subadults succumbed to the virus, and at least 1 litter of 3 was lost because their mother was diseased. This additive mortality factor (Robinson *et al*. 2015) demonstrates the vulnerability of small tiger populations to stochastic events. The SABZ population has benefited from the continuity of habitat, which has enabled immigration of tigers from surrounding areas, and with continued protection and successful reproduction, recovery is already occurring (a minimum of 20 tigers were recorded by winter 2014). For smaller tiger populations, or those that are more isolated, the likelihood of withstanding additive losses similar to those occurring in SABZ during 2009 and 2010 would be considerably lower.

The close monitoring of tigers in SABZ enables a detailed reconstruction of individual life histories of the tiger population during the period that CDV was circulating in 2009 and 2010. However, even in this intensively monitored sub-population we are limited to best-guess estimates of the impact that CDV had on the tiger population in the reserve. Beyond SABZ, tigers with confirmed and suspected cases of CDV in 2010 occurred in disparate locations 300–500-km apart, near human habitation and in distant corners of the Amur tiger's range. It is unknown whether the proximity of these tigers to human habitation increased opportunities to contract CDV, or merely the chance that cases would be reported. However, with the majority of Amur tigers occupying vast, largely uninhabited areas, it is possible that other tigers may have succumbed to CDV during the 2009–2010 period without detection. Yet with so many uncertainties relating to the epidemiology of CDV across the Amur tiger range, there is a limit to the inferences that can be drawn from the SABZ outbreak, and the extent to which the overall Amur tiger population may have been affected. Under these circumstances, population modeling can be a valuable tool to explore the key determinants that influence the impact of CDV on tiger populations. Recent models have shown that even modest levels of tiger contact with a CDV reservoir will impact population growth, and that small and isolated tiger populations are disproportionately impacted (Gilbert *et al*. 2014). Refinements of models such as this require a more detailed understanding of reservoir composition and dynamics, if they are to provide further insights into the threat to a particular tiger population.

UNDERSTANDING RESERVOIR STRUCTURE

An understanding of local reservoir structure is a critical first step to begin assessing the impact that a multi-host pathogen will have on a population, and is an important precursor to the design of management practices. Defining a reservoir is complex, but a framework proposed by Haydon *et al*. (2002, and summarized in Fig. 1) provides a useful means of conceptualizing alternative structures. All populations of tigers share habitat with a number of susceptible species that could contribute to the local CDV reservoir as maintenance or non-maintenance hosts depending on their susceptibility, population size, turnover and frequency of effective contacts. More abundant susceptible hosts are likely to have a greater contribution to CDV maintenance, and in the context of the Russian Far East this is likely to include domestic dogs, and small or medium-bodied wild carnivores, particularly raccoon dogs, *Nyctereutes procyonoides*, red foxes, *Vulpes vulpes*, Eurasian badgers, *Meles meles*, and sable, *Martes zibellina*. Tigers prey on each of these host species, providing a likely route for CDV transmission (Miquelle *et al*. 1996; Ludlow *et al*.

2014). Underscoring this potential route of exposure, rangers in SABZ reported mortalities of red foxes and raccoon dogs from an unidentified disease in both 2009 and 2010. Although tigers are largely solitary, they do interact regularly, albeit infrequently, providing a potential mechanism for tiger-to-tiger transmission (Goodrich *et al*. 2010). Aside from contact between mother and cubs, intra-specific contact is likely to be greatest between territorial tigers of the opposite sex, and in Russia these contacts occur around 1 or 2 times per month (Goodrich *et al*. 2010). In other tiger populations where tigers occupy smaller home ranges, and occur in higher densities, these interactions are likely to be more frequent, potentially increasing the rate of tiger-to-tiger transmission.

In the Russian Far East domestic dogs occur at comparatively low densities compared to other parts of the world. Due to harsh climatic conditions, feral dog populations are almost non-existent, with most animals relying on provisioning by humans for survival. Based on 2010 census data there were almost 2 million people in Primorskii Krai, of which more than 75% resided in urban centers and were, therefore, unlikely to come into contact with tigers. The remaining population is sparsely distributed across the landscape, at mean densities as low as 2.83 people/km^2. Based on preliminary estimates of human : dog ratios, this would equate to a mean density of approximately 5.10 dogs/km^2, dramatically lower than the dog density of 719 dogs/km^2 recorded in Maharashtra, India (Belsare & Gompper 2013), suggesting that the contribution of domestic dogs to the CDV reservoir may be much more important in other parts of the tiger range.

OTHER FACTORS POTENTIALLY INFLUENCING CANINE DISTEMPER VIRUS ECOLOGY IN RUSSIA

Due to the relative fragility of CDV virion to environmental conditions (e.g. heat, desiccation and ultraviolet radiation), transmission is typically thought to require close contact between infected individuals (Green & Appel 2006). However, considering the extreme cold of the Russian winter, viability could be prolonged, with the virus persisting for extended periods outside the host, raising the potential for indirect modes of transmission. Most local carnivore species will scavenge from carcasses in the forest, including tiger kills. Several carnivores, particularly canids, are known to scent mark, urinate or defecate on or around food (Goszczynski 1990), and as CDV is shed in both feces and urine, and as the virus has a half life of 9–11 days at 4°C (Appel 1987), contaminated carcasses could remain infectious for an extended period. A similar mechanism could facilitate indirect transmission between tigers, through use of urine scent marks on trees and landmarks that are regularly visited by territorial tigers of both sexes, as well as non-territory holders that may be passing through.

Although other carnivore species represent the most likely source of CDV infection for tigers, it should be noted that the virus has been associated with infections in non-carnivores, including Artiodactyls (Appel *et al*. 1991; Noon *et al*. 2003; Kameo *et al*. 2012). An outbreak of CDV in collared peccaries, *Tayassu tajacu*, in Arizona was associated with high mortality (Appel *et al*. 1991), and the virus was found to be common and enzootic in the population (Noon *et al*. 2003). While such a severe clinical syndrome has not been recorded in other ungulates, viraemia has been demonstrated in domestic pigs following experimental exposure (Appel *et al.* 1974), and antibodies to CDV (indicating prior exposure) were found in 11/41 wild boar, *Sus scrofa*, and 2/5 sika deer, *Cervus nippon*, tested in Japan (Kameo *et al*. 2012). Amur tigers prey on boar or deer with far greater frequency than carnivore species. While these ungulates may be unlikely contributors to a reservoir, they could enhance effective contact between tigers and the reservoir. A potential scenario could arise if wild boar were to contract subclinical infections when scavenging the carcasses of infected carnivores, and transmit the virus when subsequently predated by a tiger. Such a scenario remains unsubstantiated, but worthy of study.

POTENTIAL CONTROL MEASURES

Options for managing the impact of CDV infections on tiger populations will depend on the structure of the local reservoir, the mechanism of viral maintenance and the source of infection for the tigers. Intervention strategies for managing disease in wildlife are often expensive, and so it is important that control measures are weighed against the risk that CDV represents to the tiger population, are kept proportional and are achievable (Woodroffe 1999). In principal, potential management strategies could be directed at the control of disease in the target tiger population, at blocking transmission between the target and source population, or at the maintenance population(s) that contribute to the virus reservoir (Haydon *et al*. 2002). Each of these strategies requires progressively more understanding of the reservoir structure to ensure confidence of success.

Strategies directed at target populations could theoretically include treatment of infected individuals or immunization (Woodroffe 1999). At present, antiviral therapies are of limited use in treating CDV, although the development of pharmaceuticals that block the RNA polymerase enzymes utilized during CDV replication could lead to applications in the treatment of affected individuals (Krumm *et al*. 2014). This is unlikely to represent a solution in the Russian context, where there is a low probability of encountering infected tigers, but could be considered in higher density populations that can be monitored more closely.

Contemporary vaccines fall into two main categories: modified live vaccines (MLV [grown on canine or avian kidney cell lines]); and recombinant vaccines that use a canarypox vector to present CDV antigens to the immune system. Each of these has innate advantages and disadvantages. While MLVs can induce a strong and long-lasting immunity in many species, older MLVs (particularly those derived from canine cell culture such as Rockborn or Snyder Hill strains) can cause sickness and death in select taxa (McCormick 1983; Montali *et al*. 1983). New generation MLVs have been used successfully in a limited trial in lions (Kock *et al*. 1998), and offer potential for use in tigers. However, it would be important to verify their safety and immunogenicity in captive tigers before their use was proposed in a wild population. Recombinant vaccines are safer, but produce a less pronounced immune response that requires multiple doses to induce life-long immunity. One major disadvantage of both vaccine classes is that they are only available in injectable form, presenting a major challenge for delivery to most free-ranging tigers.

Strategies to block transmission from the reservoir to tiger populations are limited, particularly if wildlife constitute an important source of infection. Measures to reduce dog predation, such as preventing access to tiger habitat, could be beneficial in theory, but are unlikely to be socially acceptable where licensed hunters extensively use dogs, as they do in the Russian Far East.

Attempts to control CDV in the reservoir require a detailed understanding of maintenance host identity. Potential strategies include measures to reduce the density of maintenance populations, or to increase their immune status. Vaccination has been very effective in controlling CDV among domestic dogs in many developed countries, but may be less successful where a large proportion of the dog population is free-roaming and cannot be restrained (Belsare 2013). Strategies that target unvaccinated puppies might be more successful, as older dogs are more likely to have encountered the virus, and may be less important to CDV circulation (Belsare 2013). Reduction of dog populations through responsible ownership combined with vaccination of puppies might have the greatest chance of success. However, in situations where wildlife are important contributors to CDV, maintenance control will be extremely difficult, as the lack of an oral vaccine, and low efficacy and ethical issues associated with wildlife population control prohibit management of CDV in a wild reservoir (Woodroffe 1999).

CRITICAL STEPS NEEDED TO ASSESS AND MONITOR THE THREAT OF CANINE DISTEMPER VIRUS

As CDV is known from all countries where tigers occur, the virus represents a potential threat to wild tigers throughout their range. While the diversity of CDV susceptible hosts may vary across tiger range countries, abundant populations of domestic dogs and/or wild carnivores, acting alone or in concert, could represent a CDV reservoir, and source of infection for tigers. Wildlife managers and veterinarians in tiger range countries should be encouraged to introduce the following measures as a first step to assess the risk that CDV represents for their tiger populations:

1. Recognize and diagnose clinical cases of CDV in tigers when they occur: CDV should be considered among the differential diagnoses for any tiger that displays behavioral or neurological abnormalities. Previous cases of CDV in tigers have presented with some or all of the following: fearlessness, sensory deficits (e.g. blindness), ataxia and or muscular tremors, as well as general poor body condition. Behavioral changes, particularly loss of fear, may predispose animals to situations of human–tiger conflict. Suspected cases can be confirmed through detection of genetic sequences specific to CDV (e.g. using RT-PCR or equivalent techniques). Post mortem samples such as brain tissue has the greatest diagnostic value during the later stages of infection when infected tigers are likely to present, but other samples that may facilitate diagnosis include lymph node, lung, spleen, bladder, urine and whole blood (or fractionated blood containing leucocytes such as buffy coat). Confirmation of ante mortem cases can be more challenging, as virus may no longer be detectable in the respiratory tract or circulatory system by the time animals present. In such cases detection of virus in conjunctival or respiratory swabs, whole blood or urine would be diagnostic,

but negative results need not imply an absence of CDV infection.

2. Collect baseline data on the health of wild tigers: Every effort should be made to take full advantage of opportunities to collect samples from live or dead tigers. Collection of at least minimal sample sets including serum should take place whenever tigers are handled (whether healthy or sick), and post mortem examinations should be performed (including collection of brain tissue) whenever carcasses are found. Samples need not be analyzed immediately, particularly where laboratory resources are limited, but should be archived in secure facilities and be clearly labeled, sufficient to link material to corresponding sampling data. Appropriate storage includes freezing at or below −20 °C (for serum, fresh tissue and samples stored in media for maintaining nucleic acid such as RNA later) or maintaining at room temperature (for tissues fixed in 10% formalin). It should be emphasized that these are minimal sample sets that would be sufficient to detect antibodies to CDV (indicating prior exposure) or diagnose active CDV infections. More comprehensive sets of diagnostic samples would enable a more extensive assessment of tiger health. However, it is recognized that those involved in the handling of live or dead tigers often face a variety of constraints, including access to supplies and cold storage facilities, expertise and available time. Therefore, we encourage wildlife managers to adapt protocols, and ensure adequate supplies are available to take full advantage of sampling opportunities in their circumstances.

In the event that CDV is detected in tigers in other areas, further research would be required to assess the risk that this represents at a population level. This could include epidemiological modeling, and research directed at the reservoir to determine species composition and dynamics of CDV circulation. Such research would be vital to assessing the need for any intervention, and to identify control strategies that might be appropriate. However, ultimately, due to the problems inherent in the available control methods, and the limitations of the virus itself to spread, the most viable management strategy would be to maintain tigers in large and inter-connected populations that are able to withstand CDV outbreaks should they occur. This recommendation, of course, is in concordance with existing conservation strategies for most wildlife populations.

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