Implications of squirrelpox virus for successful red squirrel translocations within mainland UK

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Abstract
Remnant red squirrel populations in the UK mainland are threatened by squirrelpox viral disease and the reservoir of the squirrelpox virus, the invasive grey squirrel, is expanding its range. Until this threat can be effectively mitigated, there is a high risk from disease outbreaks, following proposed conservation translocation of red squirrels.

KEYWORDS
animal welfare, epidemiology, impact of disease on populations, infectious disease, pathology, reintroduction biology, Sciuridae, squirrelpox

In the later decades of the 20th century, researchers established that infectious diseases could regulate and negatively impact population numbers of free-living wild animals (Hudson, Dobson, & Newborn, 1998; McCallum & Dobson, 1995; Tompkins et al., 2001) and potentially lead to species extinction (de Castro & Bolker, 2005). Extinctions have subsequently been shown to be strongly associated with infectious diseases, for example chytridiomycosis...
in amphibians (Cheng, Rovito, Wake, & Vredenburg, 2011; Lips et al., 2006; Scheele et al., 2019). In the early part of the current century evidence from seroprevalence, experimental infection, spatial epidemiology and modeling studies (Rushton et al., 2006; Sainsbury et al., 2008; Sainsbury, Nettleton, Gilray, & Gurnell, 2000; Tompkins, Sainsbury, Nettleton, Buxton, & Gurnell, 2002) showed that squirrelpox viral disease (SQPx) has a negative impact on UK red squirrel (Sciurus vulgaris) populations through epidemics, and that grey squirrels (Sciurus carolinensis) are the reservoir host of squirrelpox virus (SQPV). Where the SQPV and grey squirrels are present, red squirrel decline is estimated to be 25 times faster than in locations where red squirrels and grey squirrels co-exist without SQPV (Rushton et al., 2006). Seroprevalence and PCR studies have shown that a high proportion of grey squirrels are exposed to SQPV (Sainsbury et al., 2000) and frequently shed it sub-clinically for extended periods (Chantrey, Dale, Jones, Begon, & Fenton, 2019). Experimental translocation of red squirrels to an area where grey squirrels were present, and controlled through trapping and culling, was initially successful but later failed due to an epidemic of SQPx (Carroll, Russell, Gurnell, Nettleton, & Sainsbury, 2009). Epidemics of SQPx continue to occur in the UK where remnant red squirrel populations are in contact with grey squirrels (Chantrey et al., 2014; Everest et al., 2017) leading to the gradual extirpation of an important part of woodland biodiversity possibly with unique haplotypes (Ogden, Shuttleworth, McEwing, & Cesarini, 2005). However, the gradual spread of SQPx epidemics across the UK mainland landscape for over 100 years (Chantrey et al., 2014; Edwards, 1962; Middleton, 1930; Sainsbury et al., 2008; Sainsbury & Ward, 1996; Shorten, 1954), suggests contact between some red squirrel populations and SQPV may be delayed for years/decades.

Over the last 10 years, there have been discussions on the pros and cons of translocating red squirrels to, and within, mainland UK for conservation purposes. We are writing to remind readers that, given the current scientific understanding of the epidemiology of SQPV in UK squirrel populations, and the absence of an effective method to permanently remove grey squirrels from proposed release areas with a suitable buffer, justifying such translocations is currently difficult. The IUCN Guidelines for Reintroductions and Other Translocations (IUCN, 2013) recommend that conservation planners should establish “strong evidence that the threat(s) which caused any previous extinction have been correctly identified and removed or sufficiently reduced.” The causes of prior red squirrel extinction have been identified but the threat in mainland UK, in the long term, remains largely unchanged because the reservoir of SQPV has a widespread and expanding distribution. The undertaking of mainland conservation translocations therefore would be contrary to recommended best practice because the original causes of decline (grey squirrel competition and the SQPV reservoir) cannot currently be managed to a point where reintroductions are justified. Any translocated population of red squirrels should be safeguarded against contact with SQPV over the long term. Failure to guarantee long-term commitments to grey squirrel eradication at appropriate spatial scales equates to a very high risk that translocations will be unsuccessful at establishing healthy viable populations due to the key reasons why the species declined in the first place.

Reduction in grey squirrel density in Wales and northern England by culling reduced SQPV seroprevalence in grey squirrel populations (4% seroprevalence, n = 28, Schuchert, Shuttleworth, McInnes, Everest, & Rushton, 2014; 27% seroprevalence, n = 160, Chantrey et al., 2014). Such management would thus likely reduce the risk to red squirrels from SQPx and provides hope for red squirrel recovery. However, even if temporary red squirrel (re-)establishment is possible in sites where grey squirrels are controlled (Schuchert et al., 2014), the fundamental problem is that the reservoir of SQPV, the grey squirrel, remains and is capable of prolific breeding and dispersal (Gurnell, 1996). Illustrating this threat, Schuchert et al. (2014) and Chantrey et al. (2019) reported high seroprevalences of SQPV in grey squirrel populations surrounding control zones (67%, sample numbers not reported, Schubert et al. 2014; 80–100%, n = 103, Chantrey et al., 2019). SQPx outbreaks in geographic regions where grey squirrels have been controlled (Carroll et al., 2009; Everest et al., 2017) are another reminder of the difficulty of managing this threat. While epidemics of SQPx are initiated through transmission of the virus from grey squirrels to red squirrels, once the virus has spilled over, they are sustained by the red squirrel population (Chantrey et al., 2014). Thus, single inter-species transmission events can cause epidemics. Unfortunately, available evidence suggests current grey squirrel culling programs do not prevent all incursions and epidemics are still to be expected (Chantrey et al., 2014) even if red squirrel and grey squirrel populations may co-exist for several years before spill-over of SQPV occurs and epidemics are seen (McInnes et al., 2009; Rushton et al., 2006; Sainsbury et al., 2008). If re-established red squirrel populations on the mainland are to be protected in the face of SQPx, ceaseless and intensive grey squirrel control operations will be needed, requiring continuous and substantial resources, unless research efforts can develop enhanced methods.

Where local grey squirrel control operations are not sufficient in scale or intensity, we thus believe that translocations of red squirrels to sites on the mainland
increase the risk of SQPx epidemics in the long term. SQPV can cause multifocal, erythematous, exudative dermatitis and cutaneous ulceration in red squirrels leading to pain and stress lasting days (Carroll et al., 2009; Sainsbury & Ward, 1996; Tompkins et al., 2002), indicating established signs of an anthropogenic welfare problem in free-living wild animals (Kirkwood, Sainsbury, & Bennett, 1994; Sainsbury, Bennett, & Kirkwood, 1995). Hence, in addition to the potential conservation failure, the consequential disease, emanating from purposeful translocation, represents a serious animal welfare concern, for which the translocation planners have a responsibility.

Efforts to better understand and mitigate the causes for red squirrel decline, including studies to remove the disease threat (for example, Ballingall et al., 2016), and continued work to design and implement consistent landscape level removal of grey squirrels could make a positive contribution to red squirrel conservation. We remain optimistic that red squirrel recovery is possible in the UK, but only once the original causes of extinction have been sufficiently managed.

CONFLICT OF INTEREST
No conflict of interest is disclosed by the authors.

AUTHOR CONTRIBUTIONS
Tony Sainsbury wrote the original manuscript. Professors Chantry, Kock and Meredith contributed to the paper with refinements regarding epidemiology and pathology. Professors Tompkins and Hudson revised the paper in the context of ecology and epidemiology. Professor Gurnell and Dr Lurz provided input on epidemiology in the context of squirrel ecology. Dr Ewen modified the manuscript with respect to reintroduction biology and with Dr Karesh, provided an IUCN perspective. Tony Sainsbury revised the paper to incorporate reviewers suggestions and received comments prior to submission from the other authors.

ETHICS STATEMENT
This paper is a review and scientific opinion piece and the work involved has not been considered by an ethical review committee.

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