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The SLOSS dilemma of road ecology: Are several small wildlife crossing structures better than a single large?

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Forum paper:

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Abstract

Crossing structures for large wildlife are increasingly being constructed at major roads and railways in many countries, and current guidelines for wildlife mitigation at linear infrastructures tend to advocate for large crossing structures sited at major movement corridors for the target species. The concept of movement corridors has however been challenged, and pinching animal movements into bottlenecks entail risks. In this paper, I address the SLOSS dilemma of road ecology, i.e., the discussion whether a Single Large Or Several Small crossing structures along a linear barrier would produce the most benefit for wildlife. I point out risks, ecological as well as practical, with investing in one large crossing structure, and list a number of situations where it may be more beneficial to distribute the conservation efforts in the landscape by constructing several smaller crossing structures; for example when the ecological knowledge is insufficient, when animal interactions are expected to be significant, when the landscape changes over time, or when future human development cannot be controlled. I argue that such situations are often what infrastructure planning faces, and that the default strategy therefore should be to distribute rather than to concentrate passage opportunities along major transport infrastructures. I suggest that distributing passage opportunities over several smaller crossing structures would convey a risk diversification, and that this strategy could facilitate the planning of wildlife mitigation. What to choose would however depend on, i.a., landscape composition and ecology, and on relationships among target species. A single large should be selected where it is likely that it can serve a large proportion of target animals, and where the long-term functionality of the crossing structure can be guaranteed. I illustrate how species and regional differences may influence the choice, using the case of ungulates in Sweden. New research is needed to

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support trade-offs between size and number of crossing structures. Cost-effectiveness analyses of wildlife crossing structures are currently rare and need to be further explored. Camera trapping and video surveillance of crossing structures provide opportunities to analyze details concerning, for example, any individual biases according to sex, age, status and grouping, and any antagonism between species and individuals. Wildlife ecology research need to better address questions posed by road and railway planning regarding the importance of specific movement routes and movement distances.

Key words: wildlife crossing structures, mitigation planning, Sweden, SLOSS

Introduction

Crossing structures for wildlife

One of the most significant ecological impacts of roads and railways are their barrier effects for terrestrial wildlife (Forman and Alexander 1998; O´Brien 2006; Beckman and Hilty 2010; Barrientos and Borda-de-Água 2017). By obstructing movements and thereby restricting the access to resources and the opportunities for migration and dispersal, linear infrastructures may inhibit the individual fitness and genetic diversity of wildlife, and negatively impact population demography and conservation status. After the emergence and growth of the applied scientific field of road ecology in the last decades (e.g., Forman et al. 2003; van der Ree et al. 2015), the barrier effects for large wildlife such as ungulates and large carnivores are now well recognized in countries worldwide (Clevenger and Huijser 2011; Wingard et al. 2014; Georgiadis et al. 2015, 2018; Collinson and Patterson-Abrolat 2016; van der Grift et al. 2018; Hlaváč et al. 2019). Accordingly, transport agencies increasingly construct adapted culverts, tunnels and vegetated bridges to provide wildlife with safe opportunities to cross major roads and railways (Iuell et al. 2003; Clevenger and Ford 2010; Rijkswaterstaat 2011; Smith et al. 2015).

Monitoring of over- and underpasses for large wildlife has provided frequent proof that they are used by a variety of species (van der Ree et al. 2007; Smith et al. 2015). In general terms, larger (wider, higher) constructions are used by larger species, by a broader array of taxa, and by a larger proportion of target populations (Rodriguez et al. 1996; Clevenger and Waltho 2000; Bhardwaj et al. 2020), although other aspects of their design may affect the frequency of use, such as human disturbances, occurrence of vegetation and cover, and siting in relation to preferred habitats (Clevenger and Waltho 2000, 2005; Ascensão and Mira 2007; Glista et al. 2009; van der Ree and van der Grift 2015; Andis et al. 2017).

Despite having recognized both the problem with barrier effects and its potential solution, in infrastructure planning practice many transport agencies still seem to consider crossing structures for wildlife to entail external or unexpected costs. Accordingly, such constructions have to be argued for on a case-by-case basis, and often end up being rather few. In response, environmental planners tend to advocate for as large wildlife crossing structures as possible, and put much effort into finding the ideal locations for those crucial constructions. This situation is reflected not least in current European guidelines for mitigation of barrier effects at transport infrastructures; many of these have their focus on methods to identify major wildlife corridors, and state ideal rather than optimal dimensions of crossing structures (Iuell et al. 2003; Alterra 2008; Jędrzejewski et al. 2009; Nowak et al. 2010; Vejdirektoratet 2011; Statens Vegvesen 2014; Ciabo et al. 2015; Reck et al. 2018; Hlaváč et al. 2019).

Size vs. number of crossing structures

While crossing structures may be necessary measures to safeguard the connectivity for wildlife across large linear infrastructures, they inevitably create bottlenecks for animal movements, irrespective of location and size. Funneling animals from larger areas into movement bottlenecks may have a number of ecological disadvantages, for example increased predation (Little et al. 2002; Mata et al. 2015) or exaggerated social interactions between animals. Moreover the concept of natural movement corridors has been criticized for lacking solid theoretical and empirical foundation (Simberloff et al. 1992), and that its frequent application in land use planning satisfies political and economic interests rather than ecological requirements (Van Der Windt and Swart 2008; Shilling 2020). For large terrestrial wildlife, well-defined, predictable migratory paths do occur in some populations (Andersen 1991; Berger et al. 2006), but seem to be the exception rather than the rule to how animals move between areas.

The size is one of the most cost driving factors for crossing structures, and in the infrastructure planning reality the cost-effectiveness of measures have to be considered. Wildlife crossing structures, from culverts to viaducts and green bridges, may range in investment cost by orders of magnitude (Sijtsma et al. 2020), and considerable savings can be made if the optimal trade-off is found between number and size of crossing structures with the aim of reaching the maximum infrastructure permeability for wildlife. While some guidelines for wildlife measures at transport infrastructures do acknowledge that a large number of narrow wildlife crossings may be more effective than a single, wide one (Iuell et al. 2003; Jakobi and Adelsköld 2011; Reck et al. 2018), the required cost-benefit analyses are rarely conducted (Sijtsma et al. 2020).

The question of size vs. number of wildlife crossing structures is analogous with that of the so-called SLOSS dilemma in conservation, i.e., the question whether a Single Large Or

Several Small protected areas would be more effective for species conservation (Diamond 1975; Simberloff and Abele 1976). That question remains a dilemma as it has no universal answer; the best strategy depends on, i.a., to what extent the smaller areas share species, on the environmental variability in and among areas, and on the distance between areas (Simberloff and Abele 1976; Akcakaya and Ginzburg 1991; Ovaskainen 2002). The SLOSS dilemma of road ecology – the trade-off between single large or several small crossing structures (Karlson et al. 2017) – is likely to share many characteristics with that of protected area designation.

The issue of SLOSS wildlife crossing structures has previously been addressed by Karlson et al. (2017), using a theoretical approach comparing outcome in model landscapes with different level of habitat contrast and aggregation. They concluded that in homogenous (low-contrast, low-aggregation) landscapes, a number of smaller crossing structures are better than one large, given that each still meets minimum ecological design criteria. This conclusion derived simply from geometry; with passage opportunities evenly distributed along an infrastructure, the distance to a crossing structure from an average point in the landscape will be shorter. In heterogeneous landscapes on the other hand, the outcome will depend on the habitat quality in and around the crossing structures; fewer animals would cross through a structure located in low quality habitat. Accordingly, in heterogeneous landscapes, more care must be taken to the location of crossing structures in relation to the habitat requirements of target species.

Aim of the paper

In this paper, I develop the SLOSS dilemma of road ecology using ecological and pragmatical arguments, and list a number of situations where it may be more beneficial to distribute the conservation efforts in the landscape by constructing several small crossing structures rather than one or few large. For the sake of tangibility, I focus on Scandinavian ungulates (moose *Alces alces*, red deer *Cervus elaphus*, fallow deer *Dama dama*, roe deer *Capreolus capreolus*, wildboar *Sus scrofa*) and large carnivores (primarily wolf *Canis lupus*, bear *Ursus arctos*, lynx *Lynx lynx*). I believe, however, that the situation described is not unique but may be applicable to other taxa and geographical regions. I conclude by suggesting how the SLOSS discussion could inform the planning of wildlife mitigation at linear infrastructures, and by proposing some directions for future research in the field.

Where and when may several small crossing structures be better than a single large?

1. In relatively intact or homogenous landscapes where animal movements are dispersed

In Sweden, natural or semi-natural habitats such as forest, wetland or mountain make up some 80% of the land area (Gerell et al. 1996). Populations of many large mammal species are currently relatively strong and range over large parts of the country (Bergström and Danell 2008; Liberg et al. 2010; Chapron et al. 2014). While most large mammals do show some preferences for forested areas, they also use agricultural land and built-up areas, particularly in nighttime when the human disturbance is low (Winsa 2008; Godvik et al. 2009; Milleret et al. 2018; Fattebert et al. 2019; Richter et al. 2020), or during seasons with available crop (Thurfjell et al. 2009; Olsson et al. 2011). In effect, these species tend to occur in most habitats and most landscapes, and their movements are less likely to be strongly funneled to specific habitat corridors or confined to certain areas.

2. In situations where the animal movement routes are expected to gradually change over time due to landscape changes

Boreal ungulates may show preferences for certain stand types in the managed boreal forest, e.g., clear-cuts, young or dense forest stands, and linear landscape elements such as riparian areas and edge zones (Winsa 2008; Thurfjell et al. 2009; Bjørneraas et al. 2011). Most of their movements, circadian as well as seasonal, are expected to occur in and along preferred habitats (Lindberg 2013; Allen et al. 2014; Bartzke et al. 2015). While these types of habitats may be stable in the perspective of a few years, they are likely to change over decades, i.e., within the expected life span of a bridge or culvert, due to forest growth or management activities. Also in less intensively managed landscapes, habitats are expected to undergo changes due to natural disturbances or succession, with potential change in animal movement patterns over time as a result. Future scenarios of climate change may further amplify changes of spatial distribution of habitats, and accordingly animal movement patterns.

3. In areas where future human development cannot be controlled, and natural habitats surrounding crossing structures may suddenly deteriorate

Animal movements may also change due to sudden human influences in the surrounding landscape. For example, new housing, mining or industry and increased outdoor recreation adjacent to crossing structures can impede their function for wildlife (Clevenger and Waltho

2000). While such developments should be addressed in landscape level physical plans and strategic impact assessment (Clevenger and Ford 2010), not all can be foreseen during the planning stage of fauna mitigation schemes. Moreover, transport agencies have limited authority over the land use outside the road or railway right-of-way, so the long-term functionality of a wildlife crossing structure depends on the compliance of surrounding landowners and land users.

4. In situations where animal movement habits simply are not known

Extensive site-specific empirical data on wildlife movements are typically difficult and expensive to access and are therefore in short supply (Clevenger and Ford 2010). Identification of movement corridors in the planning practice often have to rely on the distribution of natural or wildlife habitat, wildlife accident data or expert opinion (van der Grift and Pouwels 2006; Alterra 2008; Jedrzejewski et al. 2009; Clevenger and Ford 2010; Reck et al. 2018; Hlaváč et al. 2019; in Sweden e.g. Olsson et al. 2019). However, such indirect approaches have their flaws (Clevenger and Ford 2010; Helldin and Souropetsis 2017; Sjölund et al. 2020), and accordingly the true distribution of animal movement are often obscure.

5. When wildlife mitigation targets multiple species with different habitat choices, and no ideal site can be appointed

At some occasions, one single species is identified as the target for a mitigation scheme and the siting of a crossing structure could then be fine-tuned in relation to the habitat choice and movement patterns of that particular species. More common, however, is that wildlife crossing structures are intended to serve an entire group of species, for example ungulates or large mammals (Iuell et al. 2003; Trafikverket 2019), each having its own habits and habitat requirements. While it may be possible to identify some common patterns, such as a tendency for large mammals to dwell in larger forest tracts or other areas with less human disturbance, no ideal site for a single crossing structure can be appointed.

6. When target species are territorial or competitors, and there is a risk that some individuals or species monopolize the area in and around the crossing structure

Some large mammal species are territorial (in Scandinavia, e.g., roe deer and large carnivores; Linnell and Andersson 1998; Mattisson et al. 2011), and may therefore expel other individuals of the same species and gender from a crossing structure. Similarly, interspecific competition occur frequently among ungulates (Putman 1996; Latham et al. 1997; Feretti 2011; Pfeffer 2021; La Morgia et al. *in review*) and among carnivores (Mattisson et al. 2011), which may also lead to a dominant species effectively expelling subdominants. Although such an "ecological plug" is probably only partial, it could inhibit the movement of subdominant individuals or species through a crossing structure.

7. When target species are sensitive to hunting, poaching or predation; enemies (human or natural predators) may ambush at sites where movements of prey are pinched

Game and prey species, such as ungulates, may adapt their spatial distribution, habitat choice and activity patterns to the risk of being hunted or predated (Cromsigt et al. 2013; Lone et al. 2014, 2015; Zbyryt et al. 2018). Similarly, hunting and poaching are main causes of mortality for large carnivores in Scandinavia (Andrén et al. 2006; Liberg et al. 2012), and consequently these species avoid human interaction (Ordíz et al. 2011; Carricondo-Sanchez et al. 2020). Hunting in the direct vicinity of over- or underpasses occurs in Sweden (own observations), but how frequent this happens is not known. Incidents of natural predation on ungulates near wildlife crossing structures have been reported but appear to be rare (Little et al. 2002; Plaschke et al. 2021). Yet only the presence of ambushing predators or hunters in the area may temporarily inhibit the structure´s effectiveness for target species (Mata et al. 2015).

Implications for the planning of wildlife mitigation

The situations described in the previous section are often what infrastructure planning faces. Site-specific knowledge of animal movement patterns tends to be sparse, and in many biomes it is likely that movement routes will change over time due to natural landscape dynamics or anthropogenic impacts. With mitigation schemes targeted to multiple wildlife species it will be difficult to find the perfect site for a crossing structure, and target species are likely to interact at the site. In these cases, the connectivity delivered by each individual crossing structure cannot be guaranteed, and distributing investment over several structures would convey a risk diversification. Moreover, this is not only an economical or practical consideration; transport agencies should aim at allowing dispersed or flexible animal movements wherever they occur, and avoid the ecological predicaments that pinched animal movements may entail.

Following this line of argument, and with support from the results from the modelling approach adopted by Karlson et al. (2017), the default strategy for transport agencies should be to construct several small crossing structures rather than concentrating the passage opportunities along major transport infrastructures to a single large structure. What to choose should however depend on the context, for example the degree of habitat heterogeneity (aggregation and contrast), habitat predictability, the dimension requirements of target species, and the spatial overlap between species (Mata et al. 2005; Karlson et al. 2017). Single large may be selected at sites where it is likely that the crossing structure can serve a large proportion of target animals (species and individuals), for example where animal movements follow distinct routes, and where target species have a large overlap in habitat requirements and little social or trophic interference. However, going for single large should require that the long-term functionality of the crossing structure could be guaranteed, for example in areas that are legally protected or when solid agreements can be made with adjacent land-users to protect the crossing structure and its surroundings from significant impacts. There may be situations where an intermediate or mixed (single large combined with several small) approach may be the best choice.

A planning strategy aiming at several smaller crossing structures rather than a single large could facilitate the planning of wildlife mitigation in a few ways. It may not be necessary to put as much effort into finding the best siting or design of each crossing structure, which may save both time and costs at early planning stages. Instead crossing structures may have a standard design and be spaced out on pre-defined intervals along the infrastructure, or where the ground conditions (topography and soil) are ideal from a technical perspective. Non-wildlife bridges or culverts used by wildlife may also be included in the wildlife mitigation plan. While the goal of wildlife mitigation plans should not be to save money but to minimize wildlife–traffic conflicts, the SLOSS issue will unfold the question how to get the most out of available investments or how to reach conservation goals with a minimum of cost, and it may therefore help the matter by redirecting the focus in planning from costs to savings.

Planning for ungulate crossing structures in Sweden – a case

The Swedish Transport Administration (STA), the responsible manager for the public road and railway network in Sweden, currently works along a strategy for landscape connectivity for large wildlife that partly take a SLOSS approach, though not expressly so. According to the national ecological standards (Trafikverket 2019) safe passageways for large mammals (ungulates and large carnivores) should be provided at a maximum distance of 6 km along all major roads and railways; a requirement based on the assumption that large mammal movements are ubiquitous and dispersed, or at least ought to be so. Via supporting documents (Seiler et al. 2015 and references therein), the standards points out moose and roe deer as focal species (*sensu* Lambeck 1997); moose in particular because it is supposedly one of the most demanding large mammal species in Sweden when it comes to crossing structure design, and one of the most problematic when it comes to wildlife-vehicle accidents and barrier effects.

The standards describes a range of larger to smaller crossing structures as suitable for moose and roe deer (Seiler et al. 2015; Trafikverket 2021), and it also takes into account the predicted wildlife connectivity provided by bridges constructed for other purposes, e.g. water courses, trails and low-traffic roads (Seiler et al. 2015). Accordingly, the standards provides a framework allowing, but not requiring, that trade-offs are made between functionality and number of crossing structures.

Moose in Scandinavia are partly migratory; northwards from roughly 60°N, individuals within local moose populations conduct seasonal migrations, basically leaving upland pastures in winter to escape deep snow, starvation and predation (Sweanor and Sandegren 1988; Singh et al. 2012). Both the proportion of individuals migrating and the migration distance increase with latitude. Archaeological records indicate that moose have undertaken these migrations in the Scandinavian mountain range for thousands of years (Andersen 1991). Studies of present-day moose populations have shown that migration routes largely follow river valleys and other topographic landscape elements, and may be maintained between moose generations (Sweanor and Sandegren 1988; Lindberg 2013). While less well described in the scientific literature, also other northern ungulates in Scandinavia may conduct seasonal, directional movements along routes that are relatively stable over time, not least the semi-domestic and free-ranging reindeer (*Rangifer tarandus*; St John et al. 2016).

In the perspective of planning for ungulate crossing structures using a SLOSS approach, these regional differences would imply different output depending on the region. In northern Sweden, investing in few large crossing structures at moose migration routes may be warranted. Thorough ecological data should be collected and compiled to identify the ideal sites for these crossing structures, and considerable efforts should be made to secure their long-term effectiveness. In more southern parts of the country, sufficient permeability of infrastructures may be achieved by several smaller crossing structures, including non-wildlife bridges which tend to be plentiful along most major roads and railways.

As the current ecological standards does not recognize regional differences, nor the SLOSS approach, opportunities for better ecological function and more cost-effective mitigation measures may be missed. I suggest that explicitly integrating the trade-off between size and number of crossing structures in the planning for wildlife mitigation in Scandinavia will benefit the situation, and help achieving environmental goals regarding connectivity for wildlife.

Some implications for future ecological research

Trade-offs between size and number of crossing structures in wildlife mitigation schemes may require that road ecology research take a somewhat different angle than the current prevailing. Research and monitoring of over- and underpasses during the last decades have provided a basic understanding of how well different type of structures correspond to the demands of different species or taxa (Jędrzejewski et al. 2009; Clevenger and Ford 2010; Smith et al. 2015), but comprehensive comparisons of structures of different size and design are still few (but see Clevenger and Waltho 2005; Mata et al. 2005; Taylor and Goldingay 2010; Cramer 2012; Bhardwaj et al. 2020; Sijtsma et al. 2020). Moreover, the costs for the constructions, including any costs for planning, traffic diversion during construction, long-term maintenance etc., are rarely integrated into the analyses (Sijtsma et al. 2020). Seiler et al. (2016) and Sijtsma et al. (2020) point out some directions for how cost-effectiveness analyses of wildlife crossing structures can be set up, but the field needs to be further explored. Monitoring of wildlife-use of crossing structures should be conducted following a standardized protocol to be able to make a just comparison of the performance of a range of crossing structures, and to be able to add new monitoring results over time to a global analysis (Helldin and Olsson 2015).

A strategy to construct several small crossing structures should entail an increased demand for research on how to make also narrower crossing structures more functional for wildlife, e.g., by adapting vegetation and limiting human disturbance. However, squeezing down the size of crossing structures would also mean approaching a lower limit for functionality, and in the light of this, a much better understanding of the ecology of narrow crossing structures is needed.

I suggest a stronger emphasis in monitoring of crossing structures not only on how different species use them differentially (such as described by, e.g., Cramer 2012; Mata et al. 2015), but also differences between animal categories within species, for example between sexes and ages, individuals of different status or condition, and individuals in groups of different size and composition. It is likely that different animal individuals or categories show differences in vigilance and sensitivity to disturbance (Liley and Creel 2008), and crossing structures that consequently deter certain categories of animals are less likely to provide functional connectivity for the population, irrespective of the absolute number of individuals using the structure.

To this, we need better knowledge of what happens between animals at crossing structures, for example predation risk (real and perceived), interference competition, territoriality, dominance, and other antagonistic behaviors that can expel some target animals from the sites. The well-developed methods using camera traps and video surveillance of crossing structures provide opportunities for studying both animal categories and behaviors to a larger extent than is currently done.

Finally, I call for more efforts in wildlife ecology research to develop the knowledge of animal movements, to specifically address the questions posed by road and railway planning, of movement routes (importance of certain routes, their stability over time, and reliable methods to map them) and potential movement distances along fences to find safe passages (Bissonette and Adair 2008). While this has been studied for some large and charismatic species (e.g., moose in Sweden), these aspects are largely unknown for most species, including important target species for wildlife crossing structures.

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