The Wildlife Crossing Guilds Decision Framework: A Behavior-based Approach to Designing Effective Wildlife Crossing Structures

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ABSTRACT

Wildlife crossing structures are effective in decreasing vehicle-caused wildlife mortality and increasing wildlife movement across highways. Yet, research on effective structure designs is limited to select species, leaving uncertainty about how these data might apply to other species. Wildlife mitigation projects risk being undermined or, in some cases, overbuilt for poor cost-efficiency when there is a lack of species-specific data or an understanding of species crossing structure preferences to inform engineering design.

We classified terrestrial wildlife into eight Wildlife Crossing Guilds based on their movement, behavior and physiological needs moving through a crossing structure, and demonstrate these Guilds match up with suitable structure types to create effective passages. The Guilds derive from an extensive review of research across the globe on the factors affecting species' use of crossing structures. While taxonomic groupings and body size may act as partial surrogates for an animal's ability and willingness to use a crossing structure, we propose that the behavioral strategies species employ to maximize survival also relate to an animal's willingness to use a crossing structure, which depends on how structure characteristics affect their level of security. The Guilds synthesis is based on five primary behavioral and physiological factors influencing crossing structure use: anti-risk behavior; the need for specialized habitat conditions; movement capacity and mode of locomotion; the need for enclosure or openness; and body size restrictions. These factors underlie a species' willingness to use crossing structures, ultimately determined by an animal's ability to minimize mortality risk when passing through a structure. Where transportation biologists and planners lack wildlife crossing structure research for the array of wildlife present in a project area, the guilds lend greater confidence and cost-efficiency to wildlife crossing designs and decision-making through the purposeful application of our knowledge about wildlife biology and behavior.

INTRODUCTION

For animals seeking to cross a road, wildlife crossing structures, including bridges, culverts, overpasses and specialized structures, are widely recognized as solutions for improving connectivity for wildlife across roads and reducing wildlife-vehicle collisions (e.g., Clevenger and Huijser 2011), although further investigation into the factors influencing crossing effectiveness is still needed for many species. To date, much research in crossing structure effectiveness has centered on species that present a safety hazard to the motoring public, are of regional concern, or have special protected status. Yet even for relatively well-known species, gaps remain in our understanding of structure preferences and cost-effective design characteristics. As transportation ecolog~~i~~sts gain understanding of effective crossing designs for different species, informed decisions must be made in designing structures to ensure the best use of limited mitigation funds.

Previous studies in road ecology have proffered classifications based on major taxonomic groupings and body size as the primary determinants influencing wildlife crossing design (e.g., Clevenger and Waltho 2005; Trocmé and Righetti 2011). Bielsa and Pineau (2007) distinguished among small fauna based on their use or avoidance of underground environments, while Bissonette and Adair (2008) incorporate daily and long-distance movements to inform crossing structure size and spacing. Others have defined functional groups, which, in addition to taxonomy and body size, consider species' needs for wet or dry crossings (e.g., Grilo et al 2010), and how fragmentation impacts species with larger home ranges (e.g., Cavallaro et al. 2005, Clevenger and Huijser 2011).

Taxonomic groupings and body size may act as partial surrogates for an animal's ability and willingness to use a crossing structure, as similar species may share certain characteristics with regards to size, means of locomotion, and environmental constraints. However, taxonomic groups do not reliably account for ecological adaptations that influence crossing structure use. Deer (*Odocoileus* spp.) and pronghorn (*Antilocapra americana*) - both of the Order Artiodactyla - exhibit vastly different behaviors at crossing structures. Deer use of a variety of different structure types and sizes (e.g., Cramer 2014), while pronghorn are hesitant to use anything but the most open bridge underpasses or overpasses (Theimer et al. 2012). Similarly, lagomorphs illustrate the need for considerations beyond taxonomic group, although crossing effectiveness data are lacking. New England cottontails (*Sylvilagus transitionalis*) inhabit forest and shrub habitats with high structural complexity, and are likely to use a only passages with escape cover, whereas black-tailed jackrabbits (*Lepus californicus)* inhabit open grasslands, and are expected to require larger, more open structures with high visibility.

We suggest that the behavioral strategies species employ to maximize survival and reproductive success while reducing energy expenditures (Lima and Dill 1990) and avoiding or minimizing interactions with predators (Caro 2005) are also likely to play a role in road ecology. Specifically, we suggest that risk assessment and predator-prey dynamics (e.g., running or hiding from predators, vigilance, competition among predators, or the desire to remain undetected by potential prey or predator) relate to an animal's habitat use and movements across the landscape (Laundré et al. 2010), including their willingness to use a wildlife crossing structure as determined by how the structure characteristics affect their level of security.

Accordingly, we propose the Wildlife Crossing Guilds as a framework for informing functional wildlife crossing designs for terrestrial, semi-aquatic, aerial and arboreal fauna; it is not applicable to fully aquatic species. The guilds support practitioners in classifying wildlife into eight classes as defined by their physiological and behavioral needs. Each guild is distinguished according to five factors; (1) primarily anti-risk behavior and adaptations; (2) need for specialized habitat conditions; (3) movement capacity and mode of locomotion; (4) need for cover or openness; and (5) body size. An understanding of species' adaptations to minimize mortality risk is essential in designing crossing structures that the target species will enter and pass through, ideally with minimal hesitation, stress and energy expenditure.

The behavioral considerations encapsulated by the guilds result in a comprehensive applied approach to grouping species specifically for the purpose of informing the design of effective wildlife crossings relative to the intended target species. In developing the guilds, we analyzed existing research on the factors affecting species' use of crossing structures in order to derive generalizations based on an animal's natural history and anti-risk behaviors. The classification was first developed as part of a research project for the Washington State Department of Transportation (Kintsch & Cramer 2011) and further developed through a review of published and grey literature in wildlife and transportation ecology as well as the authors' and other colleagues collective research on wildlife movement and crossing structures around the world. Until wildlife crossing structure research is conducted for a broader array of wildlife, the guilds lend greater confidence to wildlife crossing design and decision-making through the purposeful application of our knowledge about wildlife biology and behavior.

GUILD DESCRIPTIONS

We define the Wildlife Crossing Guilds according to the degree of specialization of anti-threat adaptations as it relates to the willingness of guild members to use crossing structures. The three obligate guilds (Cover, Openness and Semi-Aquatic) require specific conditions through a structure and guild members are unlikely to pass through a structure that does not meet these conditions, even under pressure. The two generalist guilds (Medium-Structure and Large-Structure) are the most adaptive of the guilds and are tolerant of a wide variety of structure types and conditions often including hydraulic culverts with sub-optimal designs for wildlife passage. The generalist guilds are distinguished primarily by minimum structure size, although under pressure or with habituation guild members may use structures that do not meet these minimum preferences. The three specialist guilds (Conditions, Arboreal and Aerial) are highly specialized due to their physiology or movement capabilities – conditions that must be carefully addressed, as members of these guilds typically do not use structures that do not meet necessary requirements. Greater detail and documentation on the species that exemplify each of the guilds is available in Kintsch et al. (in review).

The guilds incorporate predator-prey dynamics as a key driver influencing spatial and temporal movements (Laundré et al. 2010). As different species have different detection and avoidance strategies, the functionality of crossing structures is partially contingent upon how well the predator avoidance strategies of the target wildlife are addressed. Animals are unlikely to use crossings where their predator avoidance strategies are compromised (e.g., Gagnon et al. 2011). Similarly, factors that influence predator hunting capabilities, including suitable stalking cover (Laundré and Hernández 2003) or the presence of competitors or human hunters and poachers are likely to influence predator use of crossing structures. In addition, some specialized species are limited by their movement capacity (slow vs. fast-moving), by their mode of travel (ground, water, air), or by their need for consistent environmental conditions (e.g., some amphibians) - habitat requirements that also need to be carefully addressed in structure design.

Notably, even within a species, not all populations are alike, and even the differences from one individual to the next (e.g., age, sex, size, past experience) may affect behavior (Festa-Bianchet and Apollonio 2003), including its response to a crossing structure. The degree to which an animal needs to move across a road to access resources is another motivating factor: If vital resources are available only on the opposite side of the road, an animal is much more likely to use a culvert or bridge than when the motivation is lower (Cramer 2014). Migrating populations are highly motivated to access seasonal resources, however they typically encounter structures in their migration route only seasonally. Long-term research has demonstrated that many species must learn a new structure's location, and use increases as a population becomes accustomed to a crossing structure over time (Clevenger and Barrueto 2014). Regional population variations and habituations may likewise influence responses to roads (Lewis et al. 2011; McCown et al. 2009). For example, where some wildlife populations may be adapted to human presence, others react with fear or avoidance. Similarly, the presence of predators or competitors in the landscape is known to influence wildlife activity with respect to roads (Berger 2007), including crossing structure use. While such population-level or site-specific considerations can affect crossing structure use (e.g., Sparks and Gates 2012), the Wildlife Crossing Guilds are based on generalizations across populations and provide broad guidance for application within the context of given landscape conditions.

We describe generally recommended crossing structure types and sizes for each guild with standardized terminology, and recommend that future investigations of structure effectiveness would be facilitated by common terminology and definitions. We define five general structure classes based on typical engineering breaks regarding standard sizing and wildlife use: small, medium, and large underpasses, viaducts and overpasses. Table 1 defines the minimum structure dimensions and types relevant to each structure class. Guild members generally will accept structures that exceed minimum dimensions, provided that other required features are met (e.g., cover, openness, substrate, moisture).

Crossing structures are typically described by their height and width, yet length is also a critical dimension. Wildlife crossings research is increasingly demonstrating that most species have an upper limit for structure length, beyond which crossing success declines (e.g., Australian Museum Business Services 2012, Cramer 2014). Structures 91 m (300') and longer may pass occasional animals (e.g., Bellis 2008); however, there is no evidence that structures this length or longer are used consistently by wildlife across demographic groups and in large enough numbers to provide functional connectivity. The Wildlife Crossing Guilds encapsulate the notion that as structure length increases, any unnatural or intimidating features are likely to be amplified, thereby reducing the likelihood of through-passage. Based on the compiled research, maximum structure length varies across the guilds, although, in general, longer structures (i.e., across 4-6 lanes) can be made more functional by increasing width and height to make them appear less enclosed.

TABLE 1 Standardized definitions for Structure Classes. Structure classes are defined by structure type and the minimum/maximum spans and heights. These size classes include a wide variety of types of structures with different shapes, construction materials and settings. The division between small and medium underpasses is based on typical engineering standards. The distinction between medium and large underpasses derives from the compiled research on minimum requirements suitable for mule deer and white-tailed deer passage. Note that the dimensions below do not include structure length tolerances.

Structure Size Class	Example Dimensions	Structure Types
Small Underpass Structure	≤1.5 m (5’) span by ≥1.5 m (5’) high	Pipe, box and arch culverts
Medium Underpass Structure	>1.5 m (5’) to 2.4 m (8’) span by >1.5 m (5’) to 2.4 m (8’) high	Box and arch culverts, small bridges
Large Underpass Structure	≥3.1 m (10’) span by ≥ 3.1 m (10’) high; or Lower and Wider: ≥6.1 m (20’) span by ≥2.4 m (8’) high.	Bridges and large box or arch culverts (*note*, structures with multiple chambers are considered as individual units)
Viaduct	Typically ≥ 6.1 m (20’) high over multiple spans (e.g., ≥120’ total span).	Bridges extending over multiple spans
Wildlife Overpass	Typically 40-50 m wide for multi-species crossings; may be narrower in some cases.	Overpass structure above road with soil cover; may have plant growth

Obligate Guilds

Cover Obligates

Cover Obligates are species that are reluctant to expose themselves to the predation risk of large, open spaces (Hunt et al. 1987) and whose anti-predator behavior dictates the need for escape cover in close proximity. Species that conform closely to the Cover Obligates guild include New England cottontail (*S. transitionalis*), which inhabits dense shrub habitat, and mountain pygmy possum (*Burramys parvus*), which have been documented using crossings that include a deep rock layer (Mansergh and Scotts 1989). Other guild members include a number of small mammals and some ground insects, terrestrial amphibians and reptiles.

Key Crossing Structure Attributes Effective crossing structures for this guild are small culverts located in suitable habitat with appropriate escape cover, a dry, natural pathway through the length of the structure, and natural cover adjacent to the structure openings. Guild members are most likely to use a crossing structure when the available cover inside the structure resembles their native habitat, for example, American pika (*Ochotona princeps*), which finds cover in the interstitial spaces between rocks or boulders. Cover preferences may include low vegetation, piles of brush and stumps, or burrows.

Larger underpasses or wildlife overpasses may provide passage, provided they limit exposure to potential predators by incorporating necessary cover requirements. Connolly-Newman et al. (2013) found that the placement of coarse woody debris in large mammal underpasses increased passage suitability for small mammals. In Montana, ‘vole tubes’ have been incorporated on culvert shelves through drainage culverts, successfully passing species such as meadow voles (*Microtus pennsylvanicus*), deer mice (*Peromyscus maniculatusand*) and short-tailed weasels (*Mustela ermine*; Foresman 2004).

Species Examples:

- Timber Rattlesnake (*Crotalus horridus*) were documented crossing through concrete-bottomed structures, but researchers surmised that natural substrate and habitat conditions would enhance use (Laidig and Golden 2004).
- Preble's Jumping Mouse (*Zapus hudsonius preblei*) is found along riparian corridors and open wet meadows on the Rocky Mountain Front Range. Monitoring of crossing structure use constructed by this federally endangered species have documented both adult and juvenile mice of both genders successfully passing through a 305’ long concrete box culvert with cover stations placed as stepping stones at 30’ intervals through the length of the culvert (US Fish and Wildlife Service 2013).
- Mole salamanders (*Ambystoma* spp.) have used a variety of crossing structure types, including both open top (Allaback and Laabs 2003) and closed-top tunnels (Beasley 2013). Natural soil substrate will retain moisture longer, and while salamanders will cross through tunnels with or without natural substrate, fewer individuals cross through bare concrete tunnels (Patrick et al. 2010). Cover objects for shelter and escape are important because other species such as snakes may prey on salamanders in tunnels (Pagnucco et al. 2011).

Openness Obligates

Openness Obligates exhibit extreme vigilance in avoiding potential encounters with predators and depend on long-distance visibility across open terrain or high points that afford greater visibility. Guild members are wary of potential ambushes and are less likely to use crossing structures where such features are present (Gagnon et al. 2011). This guild is characterized by species that must gauge distance to safety before entering a questionable situation, and, upon detecting a threat, depend on their ability to outrun a predator (e.g., pronghorn antelope, *Antilocapra americana*), or navigate vertical faces (mountain goat, *Oreamnos americanus*) or crags (e.g., dall sheep, *Ovis dalli*).

Key Crossing Structure Attributes Members of this guild require crossing structures with wide visual spaces, clear lines of sight through the crossings with available escape routes and, preferably, a natural substrate. Recommended crossing structures for this guild include wildlife overpasses, viaducts and, in some cases, large bridge underpasses. The greater the distance an animal must cross through a structure, the wider the structure needs to be to counteract the perception of enclosure caused by increased length. Although individual members of a population have occasionally used smaller or more confined structures – particularly where they are habituated by regular use to an inferior structure in their range – such structures have not been shown to provide functional passage for large populations (e.g., seasonal migrations) or across all age groups and both sexes of a population (Cramer 2014, Gagnon et al. 2013; Sawyer and Rudd 2005).

Species Examples:

- Elk (*Cervus Canadensis*) are highly vigilant when entering unfamiliar situations such as crossing structures. Monitoring research has well-documented elk wariness in using crossing structures, with multiple studies indicating that elk use of culverts is largely incidental (i.e., <5 animals per occurrence; e.g., Sawyer et al. 2012; Cramer 2011; Singer et al. 2011). Across the western United States, elk have displayed a distinct preference for large bridge underpasses (Cramer 2013, Dodd et al 2007) with wide visual spaces (Kintsch and Cramer 2011), and for wildlife overpasses (Clevenger and Waltho 2005, Cramer 2014).
- Pronghorn (*Antilocapra americana*) escape from predators by out-running them, and are notoriously wary approaching confined crossing structures. While individual pronghorn may occasionally pass through large, short concrete box (e.g., Plumb et al. 2003), the low visibility and openness associated with culverts are not conducive to regular use by large groups of pronghorn (Sawyer and Rudd 2005). In Wyoming, North America's largest herd of migratory pronghorn have been documented crossing two wildlife overpasses without hesitation and appear to have adapted to the structures as a part of their fall and spring migration routes in the second year following construction (Wildlife Conservation Society 2013).
- Sage-grouse (*Centrocercus* spp.) occupy open sagebrush (*Artemisia* spp.) habitat, are known to be predator wary (Hovick et al. 2014), and appear to have large openness requirements relative to their body size. The only documented use of crossing structures by sage-grouse has occurred in Wyoming through large underpasses or overpasses (H. Sawyer, personal communication). Based on habitat and anti-predator behavior requirements, we surmise that crossings for sage-grouse must be located in suitable habitat with sufficient cover and must provide good visibility to detect aerial predators.

Semi-Aquatic Obligates

Semi-Aquatic Obligates tend to seek refuge in water or travel along waterways, while not always in the water itself, these species have substantial ties to riparian and aquatic environments throughout their life history. Members of this guild include a variety of semi-aquatic mammals as well as toads, frogs and turtles.

Key Crossing Structure Attributes Members of this guild require crossing structures with accessible riparian habitat (Clevenger and Huijser 2011), and some, such as river otter (*Lontra* and *Lutra* spp.) prefer a terrestrial pathway (Carsignol 2005; Iuell et al. 2003). Members of this guild are most likely to use underpasses with streams and riparian habitat, for instance a bridge or arch culvert spanning a watercourse and its banks. Some members of this guild may tolerate crossing structures with artificial floors (e.g., metal or concrete), provided that the crossings access suitable riparian or wetland habitat on either side of a crossing structure (Clevenger and Huijser 2011). Minimum crossing structure size varies across the guild and is influenced by body size restrictions. Great Blue Heron (*Ardea herodias*) require large underpasses to accommodate their tall bodies and large wingspans (Sparks and Gates 2012), while American mink (*Neovison vison*) have used small culverts as well as larger bridge underpasses spanning stream habitat (Bellis 2008).

Species Examples:

- Mooney and Spencer (1999) found platypus (*Ornithorhynchus anatinus*) used 56 of 72 culverts investigated in suitable habitat without regard to diameter, length or slope of culverts, or depth or permanence of water, although they did exhibit a slight preference for culverts with some mud substrate present, and did not use culverts with perched outlets.
- River otters travel mostly along shorelines, although they are known to travel overland to connect between water sources. Dodd et al. (2004) documented otters using dry concrete box culverts adjacent to a wetland in Florida, while in France, otters passed through 6 m wide hydraulic culverts with a dry bench (Carsignol 2005). While otters are good swimmers, they require a dry pathway or ledge with a complete connection to embankments at the inlet and outlet.
- Wood Turtles (*Glyptemys insculpta*) depend on habitats that include clear-water streams. They have been documented crossing through open-top tunnels in Ontario (Steinberg and Whitelock, unpublished data) and a stream culvert 3 m in diameter by 26 m long (Parren 2013).

Generalist Guilds

Medium-Structure Generalists

Medium-Structure Generalists encompass a broad range of species that share a common trait of being opportunistic and adaptable to a variety of crossing structures ranging from medium to large underpasses, viaducts, or overpasses. This guild encompasses a number of medium-sized mammals (e.g., badger, coyote, fox, raccoon, skunk) as well as some terrestrial reptiles and ground birds. Medium-Structure Generalists are distinguished from the similarly adaptive Large-Structure Generalists guild by their willingness to use medium-sized culverts and bridges that are smaller and less open than what deer (*Odocoileus* spp.) are likely to use. Given the depth of research conducted on deer crossing structure preferences, these species provide a convenient and well-established size break for the guilds classification.

Key Crossing Structure Attributes Guild members demonstrate a tolerance for both more enclosed as well as more open structures, provided that there is a dry pathway through the structure and suitable habitat is accessible nearby (e.g., Ng et al. 2004). The common genet (*Genetta genetta*), for example, is described as willing to pass through any opening large enough for its head to fit (Carsignol 2005), while both gray fox (*Urocyon* *cinereoargenteus*) and red fox (*Vulpes vulpes*) appear willing to use long culverts where high traffic volumes discourage at-grade road crossings (Sparks and Gates 2012).

Though natural substrates are preferred, a number of species in this guild have been documented using structures with artificial floors, such as corrugated metal pipe culverts and concrete box culverts, provided that there is a dry pathway through the length of the structure, including fisher (*Martes pennant*; Spencer et al. 2014), bobcat (*Lynx rufus*; Singer et al. 2011), raccoon (*Procyon lotor;* Sparks and Gates 2012), and American marten (*Martes americana*; Clevenger and Huijser 2011). Concrete benches or metal shelves installed through the length of drainage culverts provide dry pathways that have also been used by a variety of guild members (Villalva et al. 2013; Foresman 2004).

Species Examples:

- Black Bears (*Ursus americanus*) have been documented using a wide variety of structure types across North America, including: paired, large arch culverts under 6-8 lanes of interstate (Kintsch and Cramer 2011); bridge underpasses (Donaldson and Schaus 2010; McCollister and van Manen 2008); medium-sized culverts (Cramer et al. 2013; Singer et al. 2011); and a 1.4 m diameter x 29 m long corrugated steel pipe (Sierra National Forest 2012-2013, unpublished data).
- Bobcats are found in a variety of habitat types and have been documented using a wide variety of structure types. Cramer (2014) found bobcats equally present at bridges and culvert structures in Utah. In Colorado, bobcats were documented crossing through partially sediment-filled pipe culverts (Singer et al. 2011).
- Koalas (*Phascolarctos cinereus*) have been recorded crossing through bridges and culverts (3 m x 3 m and larger), provided the culvert is not too long, has a dry pathway or shelf, and adjacent habitat (Australian Museum Business Services 2012). The presence of 'furniture' (i.e., raised wooden structures) through an underpass can provide increased security and an escape from predators (Australian Museum Business Services 2012; Jones et al. 2012).

Large-Structure Generalists

Large-Structure Generalists tend to be very mobile species that typically respond to risk with behaviors such as intimidation, distraction, grouping or fleeing. Guild members include large carnivores, large-bodied yet adaptable species, such as moose (*A. alces*), and kangaroos and wallabies (*Macropodidae* family), which are adaptable to a variety of structure types and sizes (Bard and Jones 2013), provided the structure is high enough so that the animals may stand upright and hop unimpeded (Blacker 2014). Jackrabbits (*Lepus townsendi*) and hares such as the Iberian hare (*Lepus granatensis*) are also included in this guild for their demonstrated preference for large, open structures, particularly relative to their body size (e.g., Cramer 2014; Mata et al. 2008, respectively).

Key Crossing Structure Attributes The animals in this guild are characterized by a willingness to use many types and sizes of structures that meet a minimum size requirement, including large underpasses, (bridges, large box and arch culverts), viaducts or overpasses. Effective underpass designs for this guild are typically wide as they must provide good visibility and clear sight lines through the structure and, preferably, have a natural substrate. Large-Structure Generalists do not require as much visibility through a crossing structure as Openness Obligates. While bridge structures may be preferred, all of the species in this guild are also known to use arch or box culverts.

Species Examples:

- Mule deer (*Odocoileus hemionus*) have been documented passing through a variety of structure types and sizes, provided they meet minimum size constraints and are not too long or tunnel-like. Cramer (2014; 2013) and Schwender (2013) found that as the length of culverts increased, the rate of repellence also increased.
- Mountain Lion (*Puma concolor*) are stalking hunters that reportedly prefer open span bridges over culverts and overpasses (Gloyne and Clevenger 2001), yet mountain lions have been documented passing through a variety of structure types that offer good visibility, including overpasses, bridges and culverts in Utah (Cramer 2014) and bridges and culverts in Colorado (Singer et al. 2011). Structure use is correlated to high quality habitat (Gloyne and Clevenger 2001), although other landscape factors (local terrain, traffic volume, fencing) may also play a role in structure use (W. Vickers, personal communication).
- Grizzly Bear (*Ursus arctos*) in Banff have demonstrated adaptability to a variety of crossing structure types and sizes, although medium-sized underpasses were rarely used (Clevenger and Barrueto 2014). Clevenger and Huijser 2011 note a preference for large, open structures with good visibility, such as overpasses and large span bridges. In Montana on US 93, grizzly were documented using large arch culverts (W. Camel-Means, personal communication).

Specialist Guilds

Conditions Specialists

Conditions Specialists require individual consideration to meet unique crossing needs due to their specialized mobility, habitat or environmental constraints. Conditions Specialists employ a diversity of anti-risk mechanisms and behaviors, and include extremely low mobility species (e.g., mollusks); permeable-skinned species (e.g., amphibians), which require consistent and specific ambient conditions; mass migrating invertebrates, such as the Christmas Island red land crab (*Gecarcoidea natalis*) and male tarantulas (*Aphonopelma hentzi*); or other species with specialized needs or movement capabilities.

Key Crossing Structure Attributes Effective crossing structures for Conditions Specialists must provide species-specific habitat conditions that closely resemble their natural habitat to reduce risk and exposure. These attributes are best addressed via specialized crossings, or in some cases these attributes may be integrated into a larger, multi-species structure. Because Conditions Specialists are by definition highly specialized, these guild members may require novel elements and crossing designs to accommodate their passage needs.

Species Examples:

- Northern leopard frogs (*Lithobates pipens*) are found in various terrestrial and freshwater habitats and escape predation by jumping into water. Substantial terrestrial movements occur during seasonal migrations between wetlands. In an experimental study, Woltz et al. (2008) documented a willingness to use longer pipes (9.1 m), but a preference for shorter pipes with moisture-retaining soil substrate and greater light permeability, such as open-top pipe culverts.

- Christmas Island red land crabs (*Gecarcoidea natalis*) are known for their mass migrations to the coast for spawning at the onset of the rainy season. While, individually, crabs are small and mobile, the nature of this migration requires crossings that can accommodate large numbers of crabs at one time. Grated, open-top culverts with natural substrate and connected with drift fencing effectively funnel crabs to safe crossing locations under roads. In addition, specialized 'crab bridges' have been erected, allowing crabs to climb up and over road traffic.
- Terrestrial invertebrates (e.g., mollusks, snails and slugs) are considered Conditions Specialists due to their extremely low mobility. On I-90 in Washington, crossing structure designs integrated precise habitat conditions to accommodate the need for several generations to live on an underpass or overpass (Washington State Department of Transportation 2006).

Arboreal Specialists

Arboreal Specialists move across the landscape primarily through the tree or brush canopy rather than on the ground surface, providing them with a specialized mechanism for escaping from predators. Guild members include monkeys, gliders, arboreal voles, some bats, tree-dwelling marsupials and understory birds.

Key Crossing Structure Attributes The most effective crossing designs for these species are large viaducts spanning continuous natural canopy cover, overpasses with planted vegetation or canopy-level structures over a roadway, such as a metal or rope treetop bridge. Glider poles have improved cross-roadway movements for squirrel gliders (*Petaurus norfolcensis*) in Australia (Goldingay et al. 2011) and for Carolina northern flying squirrels (*Glaucomys sabrinus coloratus*) in North Carolina, USA (Kelly et al. 2013). Studies suggest that rope bridges installed over a roadway, under a road through a creek bridge, or atop a wildlife overpass may restore connectivity across roads for a variety of arboreal mammals (Goldingay et al. 2013, Teixeira et al. 2013). Shorter rope bridges (15 m) may facilitate a greater number of passages than those 40 m or longer (Weston et al. 2011), depending on the target species.

Species Examples:

- Arboreal primates, including Black lion tamarin (*Leontopithecus chrysopygus*), used a wooden pole bridge structure in southern Brazil (Valladares-Padua et al. 1995), while Teixeira et al. (2013) reported brown howler monkey (*Alouatta guariba clamitans*) use of canopy rope bridges. Such canopy bridges designs must consider the weight and size of the target species, as well as the way the animal moves and the distance between its limbs.
- Carolina Northern Flying Squirrel (*Glaucomys sabrinus coloratus*) are successfully using tall poles with launch platforms that allow them to glide across the Blue Ridge Parkway in North Carolina (Kelly et al. 2013).

- Canopy-dependent species are likely to move across narrow roads between tree canopies if the tops are close together (Taylor and Goldingay 2004). In Europe, understory woodland birds used wildlife overpasses with planted vegetation significantly more to cross highways than direct overflights over open roads (Keller et al. 1996). Pell and Jones (2015) also found some birds crossed highways significantly more frequently on overpasses, especially species that are unsuited to sustained direct flight.

Aerial Specialists

Aerial Specialists are species whose primary means of movement is flight: birds, bats and flying insects. Despite their ability to fly over roads, many birds appear sensitive to landscape fragmentation and the increased energy costs and depredation risk involved in crossing habitat gaps.

Key Crossing Structure Attributes Crossings mitigation for this guild include viaducts spanning habitat areas that allow guild members to continue their flight paths beneath the road, and appropriately vegetated overpasses (Jacobson 2005). Smaller bridges with less light and discontinuous vegetation may be less successful in passing Aerial Specialists, as researchers found with a bridge initially thought to be high enough to permit dragonfly passage (K. Lah, personal communication). An alternative to large crossing structures spanning natural habitat is to direct Aerial Specialists over the flow of traffic.

Species Examples:

- Bats (Order Chiroptera) regularly use culverts and bridges for commuting and foraging. A study in the United Kingdom documented greater horseshoe bat (*Rhinolohus ferrumequinum*) was documented using culverts under a new roadway on only a few occasions, although the authors speculated that use may increase over time (Wray et al. 2005). This study also found that when lesser horseshoe bats (*R. hipposideros*) encounter a roadside fence barrier they tend to fly up and over it and immediately return to their original flight path height in the line of traffic; Whereas they are more likely to follow a higher flight path where a gentle slope is place to guide them up and over traffic.
- Experiments with Hines emerald dragonfly (*Somatochlora hineana*), an endangered species, tested barrier fencing as a means of diverting flight higher than the flow of traffic with some success (Furness and Soluk 2015). An interstate bridge spanning dragonfly habitat considered high enough to allow flight underneath the bridge had little success in passing dragonflies, possibly due to less light through the crossing (K. Lah, personal communication).
- Royal terns (*Sterna maxima*) are at increased risk of vehicular collisions when bridges and causeways are perpendicular to the predominate wind direction, causing downdrafts. Aluminum fence poles spaced at regular intervals along the edge of a bridge create an apparent barrier and cause birds to fly higher, over the flow of traffic (Jacobson 2005; Bard et al. 2002).

APPLICATIONS

An understanding of crossing structure size requirements and characteristics for each Wildlife Crossing Guild provides transportation biologists and other practitioners with initial guidance for designing crossing structures. Figure 1 provides a flowchart to guide users through the process of identifying a species' guild affiliation. Once the guild(s) of the targets species are identified, users can hone in on key crossing structure design elements, including structure type, size requirements, substrate and other features. While any given crossing structure design will depend on a variety of site-specific factors, such as terrain, hydrology and landscape context, the guilds framework highlights the most essential elements of crossing structure design relative to the site's target species.

Where a species exhibits characteristics from two guilds, crossing structure requirements may combine recommendations for both guilds. For example, adult mole salamanders (*Ambystoma* spp.) largely occupy burrows and require flat rocks or woody debris through culverts to provide cover from predators such as snakes; this feature is a key attribute of the Cover Obligates guild (Pagnucco et al. 2011). However, salamanders also require moisture through a culvert, where they are at risk of desiccation (Jackson et al. 2015), and may require special design features, a characteristic attributed to Conditions Specialists.

In some cases, a species may tolerate a sub-optimal structure, although species-specific enhancements may increase use of a structure by more individuals. In all cases, additional analysis is required as the Wildlife Crossing Guilds provide general guidance useful at the initial stages of planning and design. Detailed structure designs will ultimately depend on population and site-specific considerations for accommodating diverse species arrays or regional variations in species preferences due to the presence or lack of predators, resource availability, human activity, noise or other considerations.

Where multiple target species representing several guilds are present, structure design characteristics can be combined to address the range of species' movement needs. The specific design elements required by each target guild must be individually addressed: A larger structure will not automatically accommodate small animals if it does not provide appropriate cover or other necessary attributes. Where uncertainty remains regarding crossing structure type and dimensions, practitioners are cautioned to design more inclusive structures that are more likely to capture passage needs for all members of a population, particularly when addressing the movement needs of rare species.

The guilds decision framework offers an important starting point useful in the early stages of road corridor or project level planning where information regarding structure type and size can be used to inform wildlife mitigation design and budgeting. For example, projects in several New England and western U.S. states and Israel have adopted the guilds framework to preliminarily identify retrofit opportunities and new crossing structure needs for improving habitat connectivity for wildlife (e.g., Kintsch and Cramer 2011, Kintsch et al. 2011).

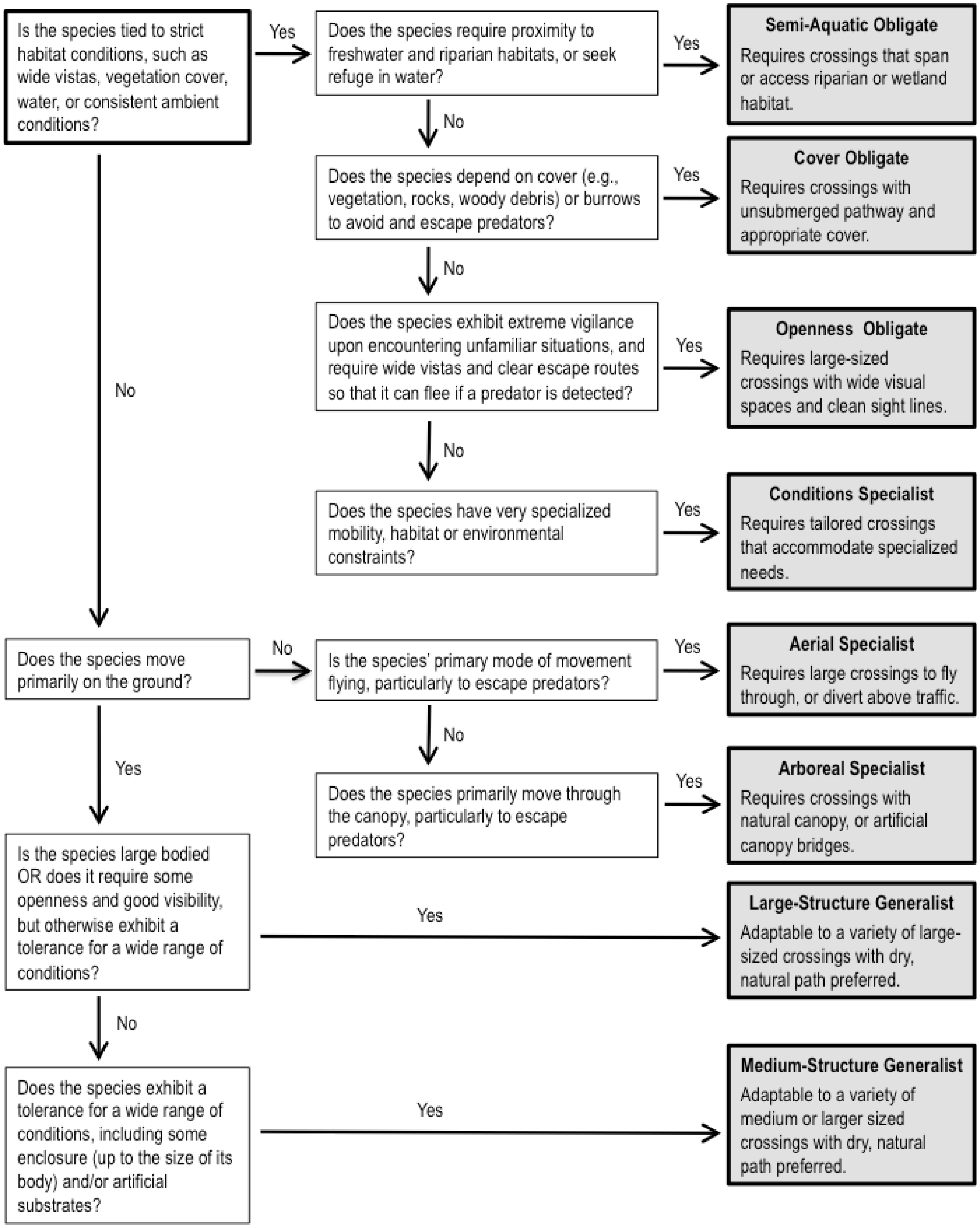

FIGURE 1 Flowchart for classifying species into the Wildlife Crossing Guilds. Once a species is classified into the appropriate guild, practitioners can use this information to determine minimum crossing structure requirements and key design features.

CONCLUSIONS

Wildlife crossing projects risk being ineffective or, in some cases, overbuilt, resulting in poor cost-efficiency when there is a lack of species-specific data on structure preferences to inform project planning and engineering design. Simple species groupings based largely on taxonomy and body size do not adequately capture species' behavioral drivers and risk management needs. The Wildlife Crossing Guilds provide a conceptual framework for informing species' preferences based on natural history and behavioral characteristics. By classifying target species into guilds based on their adaptations to avoid perceived risk, practitioners can readily identify key components of a suitable crossing structure, including shape, size and habitat features, to feed into project designs. The guilds lend focus for discerning among species with the most restrictive requirements while also identifying those that are more adaptable to a range of conditions. Using this framework, mitigation measures can be built to meet the needs of the target species and guild while also ensuring cost-effective mitigation designs (Trocmé and Righetti 2011).

Ultimately, crossing structure effectiveness depends on a variety of site-specific factors including structure placement relative to species' movement patterns (Land and Lotz 1996), the presence of adjacent high quality (Gloyne and Clevenger 2011, Ng et al. 2004), and access to seasonal habitat and resources. In addition, species-specific wildlife barrier fencing designed to guide animals to crossing structures has been shown to increase passage rates (e.g., Woltz et al. 2008, Dodd et al. 2007).

Applying this understanding of specific life strategy requirements to the design of crossing structures draws on knowledge of a species' behavioral instincts to avoid compromising their level of safety and comfort when crossing through a structure, notably, their ability to detect and escape predators or competitors, or avoid other types of risk. The guilds approach offers a decision tool that resource and transportation practitioners around the world can use when evaluating existing or potential infrastructure mitigation for wildlife permeability. This framework is particularly useful when data regarding species-specific crossing structure performance are inadequate.

The Wildlife Crossing Guilds concept will benefit from further research on species' crossing structure preferences under different conditions and the factors that affect crossing success across species. We encourage practitioners to apply and consider refinements as future studies lend further clarity to crossing structure preferences, particularly by species with currently unknown passage history.

BIOGRAPHICAL SKETCHES

Julia Kintsch is Principal and Conservation Ecologist at ECO-resolutions, and certified Senior Ecologist with the Ecological Society of America. Julia specializes in conservation planning, road ecology, and the collaborative processes needed to achieve conservation objectives across large landscapes. In 2008, Julia launched ECO-resolutions to work directly with transportation and wildlife agencies in planning and designing for landscape connectivity, including wildlife linkage analyses, mitigation design, and effectiveness monitoring.

Sandra Jacobson is a wildlife biologist for the U.S. Forest Service, Pacific Southwest Research Station. She currently serves as a subject matter expert for transportation ecology across the country. Her projects have won Exemplary Environmental Initiatives in 2009 and 2012 from FHWA, a Telly Award for the 2013 video on Avoiding Animal-Vehicle Collisions, and the 2015 FHWA Environmental Excellence Award for Environmental Leadership as part of the ARC Solutions steering committee. She has worked on highway projects on 18 National Forests.

Patricia Cramer is a wildlife researcher in transportation ecology. She works with state departments of transportation and wildlife agencies to help research and design the best wildlife crossing and mitigation measures, and to bring wildlife into the transportation planning process. Her work has earned awards from Utah Department of Transportation (2015), Federal Highways Environmental Excellence Awards (2013, 2011), Utah Wildlife Society (2013), the Mule Deer Foundation (2012), and the Denver Zoo (2010).

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