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Green bridges in a re-colonizing landscape: Wolves (*Canis lupus*) in Brandenburg, Germany

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Abstract

Gray wolves (*Canis lupus*) are recolonizing many parts of central Europe and are a key part of international conservation directives. However, roads may hinder the reestablishment of gray wolves throughout their historic range by reducing landscape connectivity and increasing mortality from wildlife-vehicle collisions. The impact of roads on wolves might be mitigated by the construction of green bridges (i.e., large vegetated overpasses, designed to accommodate the movement of wildlife over transportation corridors). In this study, we investigated the seasonal and diurnal use of a green bridge by wolves and three of their main prey species: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*). We found that all four species used the green bridge. Wolves were most active in winter, whereas prey species were most active in spring and summer. All species were more active at dusk and during the night than at dawn and during the day. We found no evidence that wolf presence influenced bridge-use by prey species, consistent with other tests of the prey-trap hypothesis. Our results suggest that green bridges are used by wolves and prey species alike, and may foster connectivity and recolonization for these species in rewilding landscapes.

KEYWORDS

Canis lupus, connectivity, habitat fragmentation, human-wildlife conflict, predator–prey dynamics, recolonization, road ecology, wildlife corridors, wildlife monitoring

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1 | INTRODUCTION

Roads can have a number of negative impacts on wildlife, such as habitat loss and fragmentation, barrier effects and loss of landscape connectivity, and mortality due to collisions with vehicles (Forman, Sperling, Bissonette, & Clevenger, 2003; Jaeger et al., 2005; Eigenbrod, Hecnar, & Fahrig, 2009; van der Ree, Smith, & Grilo, 2015). These impacts can be mitigated using crossing structures such as green bridges (Bissonette & Adair, 2008; Forman, 2012; Karlson, Seiler, & Mörtberg, 2017; Smith, van der Ree, & Rosell, 2015). Green bridges (wildlife overpasses) are large, vegetated structures designed to reduce the risk of wildlife mortality while improving habitat connectivity by facilitating the safe passage of wild animals from one side of a road to the other and reducing the exposure of individuals to traffic (Iuell et al., 2003; Smith et al., 2015). They can support the movement of multiple species (Clevenger & Waltho, 2005) and demographic classes (Ford, Barrueto, & Clevenger, 2017) and thus offer support in conservation or protection of a broad variety of species from the impacts of roads.

Gray wolves (*Canis lupus*) have returned to Germany from Poland after their local extinction in the 19th century (Chapron et al., 2014), due to the successful implementation of European and national conservation laws (e.g., the Bern Convention, Fauna-Flora-Habitat [FFH] Guideline, and BNatSchG). As the wolf population continues to grow, young animals disperse at increasingly long distances to find new and unoccupied territory (Mech & Boitani, 2003). In a landscape predominated by agriculture, intensive forestry, and urban developments, safe road crossings can be challenging. Road-associated mortality accounts for approximately 76% of total confirmed wolf mortality in Germany (of 485 dead wolves in total; DBBW, 2020b). Green bridges may be a solution to address the impacts of roads on wolves (Beckmann, Clevenger, Huijser, & Hilty, 2010; Clevenger & Huijser, 2011; Clevenger & Waltho, 2005), however the use of green bridges by wolves in the rewilding landscape of Eastern Germany has not been studied.

Wolves use of green bridges vary seasonally and diurnally, and if the wolves are alone or in a pack. For example, lone wolves may use the bridge in winter as they disperse to find new territory (Mech & Boitani, 2003), but wolf packs may show little seasonality in use. Wolves are also less likely to be active according to their ecology. Use of crossing structures by wolves may also be related to the other species using the structure (Ford & Clevenger, 2010). For example, wolves may cross more during the night than during the day in order to avoid human contact (Barrueto, Ford, & Clevenger, 2014). There may also be relationships between when wolves and prey species, such as red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), use the structure, as prey may avoid the bridge when wolves are active (Caro, 2005; Tambling et al., 2015). Understanding when wolves use green bridges may provide insights into the potential use of green bridges to improve landscape connectivity and facilitate habitat expansion for wolves.

In this study, we investigated wildlife use of a green bridge in Brandenburg state, Germany, to identify seasonal and diurnal use patterns of wolf and prey species. The bridge was constructed in 2012 (BAST, 2014) to provide connectivity and reduce the barrier effect for species travelling north–south. Camera trap monitoring has shown regular use by various species, including wolves since late 2015 (LFE, 2019); however, a systematic evaluation of species usage and effectiveness has yet to be conducted. We aimed to asses: (a) the temporal trends in green bridge use by wolves; (b) the temporal trends in green bridge use by three prey species of wolves: red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*); and (c) the temporal correlation in green bridge use between wolf and prey species. We predicted that: (a) wolves would use green bridges more in winter when subadults disperse to find new territory (Mech & Boitani, 2003); (b) wolves would cross more during the night than during the day according to their ecology and because they may avoid human contact (Barrueto et al., 2014); and (c) there would be clear divisions in the temporal and seasonal uses of the crossing structure between wolves and their prey species, as prey might avoid the structure when predation risk is high (i.e., when wolves are active on the structure; Caro, 2005; Tambling et al., 2015; Ford & Clevenger, 2010). Using these data, we provide insights into bridge use by wolves and prey species, and comment on the potential to use green bridges to minimize road-associated mortality and support the re-establishment of wolves through their historic range in Germany.

2 | MATERIALS AND METHODS

2.1 | Study area

We conducted this study in Brandenburg state in eastern Germany (Figure 1). Brandenburg has large areas of intense agriculture (49% of total area) and forest (35%). The remaining 16% are largely developed or urban areas (Amt für Statistik Berlin-Brandenburg [Statistics Department Berlin-Brandenburg], 2018). Brandenburg state currently hosts the largest wolf population in Germany; 41 of Germany's 105 wolf packs were located within state borders in 2019 (König et al., 2020). Between 2006 and 2015, the wolf population grew at a steady pace of approximately 36% per year (Reinhardt et al., 2019), and by 2018, much of the southern extent of Brandenburg state was occupied by wolves (DBBW, 2020a).

The focal green bridge in this study crosses over Highway A12. Highway A12 is a major highway that connects

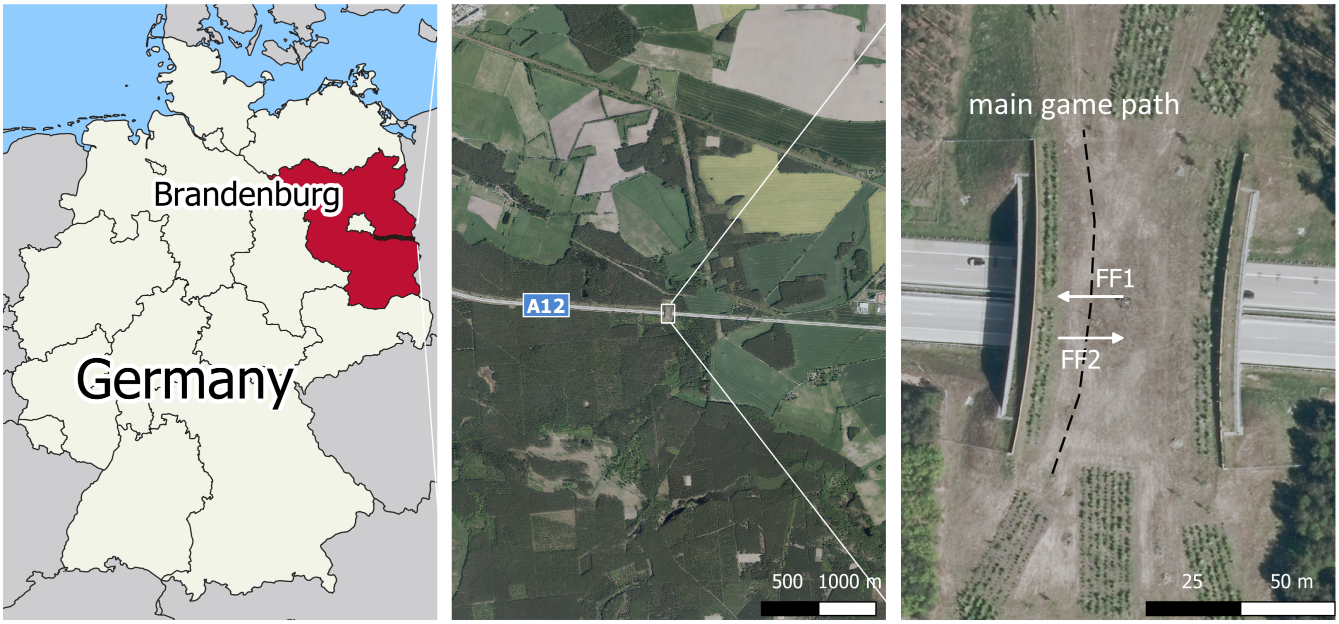

FIGURE 1 Location of the green bridge and study design. Left: Map of Germany. A12 shown in black within Brandenburg state (red), other German states shown by thin black lines. Middle: Aerial image of the landscape surrounding the green bridge, with A12 bisecting the middle of the panel. Right: Aerial image of the green bridge, with the wildlife camera (FF1/FF2) locations shown and arrows indicating the viewing angles of the wildlife cameras. The dotted line indicates the main wildlife game path. © GeoBasis-DE/LGB, dl-de/by-2-0

Berlin to the Polish border (Figure 1). On average, the highway is 31 m wide and supports 30,000 to 40,000 vehicles per day with four lanes (two in each direction). It is completely fenced to reduce access of wildlife to the motorway. The green bridge is 50 m wide, and vegetated by shrub borders, to minimize traffic noise on the bridge, and young trees in the middle of the bridge. The green bridge connects a large pine forest (partially deciduous woodland) in the south to a small band of woodland followed by an open agricultural landscape in the north (Figure 1). The forests are managed by the Forestry Department of Brandenburg (LFB). Recreational use is allowed in the forests, but it is not very frequent since the forests are large and dense, and this region has a relatively low human population density. Crossing of the green bridge is prohibited for the public. When the bridge was constructed in 2012, wolf packs were absent in the region. In December 2015, the first two wolf crossings were observed, followed by 85 wolf crossings in 2016 (LFE, 2019). Since then, wolves have regularly used the green bridge (LFE, 2019). Since 2014/2015 there are two known wolf packs present south of the bridge (DBBW, 2020a).

2.2 | Data collection

We collected data between October 2017 and October 2018. We installed two Dörr SnapShot Limited cameras 20 m apart from each other along a wildlife path (Figure 1). These cameras capture multicolored pictures throughout the day and are supplemented with infrared light for nighttime image capture (Dörr GmbH, 2020). Cameras were set to normal sensitivity, installed approximately 1 m above the ground and positioned to face opposite directions (FF1 faced westward, FF2 faced eastward) to cross-check the photos and verify the number of individuals crossing at the same time. FF1 was programmed to take two pictures per trigger, with a recharge time of 30 seconds. FF2 was programmed to take one picture per trigger, with a recharge time of 1 min. The different settings for the second camera were chosen to avoid large numbers of empty shots due to thermal influences such as direct sunlight, which is a known problem for wildlife cameras (Gužvica et al., 2014). Data were collected every 2 weeks.

2.2.1 | Identifying crossing events

All photos were analyzed for focal species, number of individuals, time of day, date, and direction of movement. Human presence on the bridge was also recorded and used to investigate the impact of human activity on the presence of wildlife. Given the placement of the cameras and bridge, we collected data on northward and southward crossing. We identified "crossing events" as sequences of pictures in which individuals or a group travelled in one direction, and did not return within a time span of 1 min. Individuals of the same species were counted as a group/pack when at least two individuals were recorded within a time span of 5 min and they were traveling in the same direction. The timeframe of 5 min was selected as a compromise between the approaches of Barrueto et al. (2014), who used 2 min, and Šver et al. (2016), who used 10 min. There was no evidence on our cameras of an animal turning around and returning from the direction they approached the cameras without crossing the bridge completely.

2.2.2 | Temporal data collection

We analyzed crossing events on two temporal scales: seasonal and daily. Months were classified into the following seasons: winter: December–February; spring: March–May; summer: June–August; and autumn: September–November. Daily activity was categorized into four periods, according to dusk and dawn in each season: night: night–dawn, dawn: dawn–day, day: day–dusk, dusk: dusk–night (for hourly divisions, see Supporting Information, Table S1). We used time of day relative to the amount of daylight (i.e., the sun's position) to identify the time periods as that most likely corresponds with natural crepuscular and nocturnal activity patterns in these species. We explored seasonal variation to explore if seasonal patterns correlated with dispersal activity in wolves—an event which occurs predominately in winter. Daily activity was investigated to see if predators, prey, and humans showed any pattern of use that could be dependent on one another, for example, prey avoiding the bridge during high wolf use, and wolves avoiding the bridge during high human use.

2.2.3 | Identifying wolf-prey interactions

To identify wolf-prey interactions, we determined all events where prey (red deer, roe deer, or wild boar) and wolves used the bridge after one another. For each interaction event, we identified if wolves crossed before or after the prey species. We used the time between events to infer if there was any relationship between species, since we did not capture any direct interactions on our cameras. If time elapsed in wolf-following-prey events is significantly different than the time elapsed in prey-following-wolf events, there is suggestion of interaction between wolves and their prey (Ford & Clevenger, 2010). Should the time elapsed between events not differ between predator and prey, it can be concluded that there is a weak or absent interaction on the green bridge (Ford & Clevenger, 2010).

2.3 | Data analysis

2.3.1 | Temporal trends in green bridge use by wolves

To investigate seasonal and daily patterns in crossings by wolves, we explored if the crossing behavior differed between times of the day and between seasons using two steps. First, we observed if the number of wolf crossings changed between time of day and seasons. We used a Poisson regression model to estimate the number of crossings, using the time of day and season as explanatory variables. To observe if this relationship was different between lone and packs of wolves, we conducted models on the entire dataset, and on the lone or pack data separately.

Second, in order to determine if the direction of wolf crossings changed with time of day and seasons, we fitted binomial regression models using the occurrence of a crossing northward as the response variable and season and time of day as explanatory variables. We used a binomial model because the options were to travel north (1) or south (0), and we used south as the reference observation because northward travel could be related to dispersal or territory expansion behavior. The wolf crossing data were split between overall, lone and packs of wolves to determine if there was any evidence of dispersal behavior. In the model that incorporates the overall data, we used a binary term of lone wolf (1) or pack (0) as an explanatory variable, as well as season and time of day. If wolves crossed northbound more than southbound, this may indicate an expansion of territory or a dispersal behavior, particularly if it is a lone wolf, whereas when northbound and southbound crossings were equal, this may indicate that the bridge is within a territory and used for daily movement and hunting.

2.3.2 | Temporal trends in green bridge use by prey species and humans

To investigate seasonal and daily patterns in crossings by red deer, roe deer, wild boar, and humans, we explored if the crossing behavior differed between seasons or between times of the day. Similar to the analysis on wolf crossings, we used a Poisson regression model to estimate the number of crossings, using season and time of day as explanatory variables. We conducted a different model for each species.

2.3.3 | Wolf-prey interactions

To investigate wolf-prey interactions, we fitted gamma regression models using minutes between events as the response variable and the event type (wolf crossing before or after prey) as the explanatory variable.

All analyses were performed using R v.3.5.3 (R Core Team, 2019). Models were fitted using "glmer" from the "lme4" package (Bates, Machler, Bolker, & Walker, 2015). In the temporal models (both for wolf and prey) the global models included season and time of day. We used the "dredge" function from the "MuMin" package (Barton, 2019) to determine the best candidate model and the relative importance of both coefficients, based on the lowest AICc. We used AICc due to relatively low sample sizes (Burnham & Anderson, 2002). When multiple top-performing models were identified (i.e., $\Delta AICc \leq 2$), we used model averaging to estimate model outputs (Burnham & Anderson, 2002). If only one top model was identified, we used estimates corresponding to that model.

3 | RESULTS

We collected 50,159 photos over the study period (FF1 $n = 25{,}909$; FF2 $n = 24{,}250$). Photos that were blank (i.e., contained no animals or humans, $n = 45{,}446$) or in which the animal was unidentifiable ($n = 63$) were excluded from the analysis. The remaining 4,650 pictures contained the following and were included in our analysis: wolves ($n = 396$), red deer ($n = 3{,}200$), roe deer ($n = 204$), wild boar ($n = 112$), and people ($n = 398$). We identified 931 crossing events: 111 by wolves (65 individuals, 46 wolf packs), 431 by red deer, 106 by roe deer, 41 by wild boar, and 43 by humans (21 by maintenance staff/researchers and 22 by civilians; see Supporting Information, Table S2). In 11 events, the crossing direction of animals could not be determined because the pictures taken were too dark or blurry to identify the species, so these events were not included in the subsequent analysis. Humans were never recorded crossing the bridge during dawn or night, so those categories are excluded in the time of day analyses.

3.1 | Temporal trends in green bridge use by wolves

Overall crossings by wolves were best described by models that included time of day and season. For lone wolves, the top model included only time of day, and for packs of wolves, the top models include time of day and season (Table 1). Overall crossings were lowest in the autumn during the day (intercept; Figure 2; Supporting Information, Table S3). Crossings during dawn, dusk and night were significantly greater; crossings during spring and summer did not differ significantly, however, crossings during the winter were significantly greater. Lone wolves crossed the least during the day (intercept), and significantly more during dawn, dusk and night. Finally, packs of wolves crossed more during the dusk and night compared to dawn and day, and their crossing rate over the year did not significantly change among seasons. However, there was an, insignificant, tendency for packs to cross more during the winter.

The overall probability of wolves crossing towards the north was best described by a model that included the time of day and if the crossing was by a lone wolf or wolf pack (Table 2). The probability of lone wolves travelling north was also best described by time of day, however the probability of packs of wolves travelling north was not well described by season nor time of day, and the null model described this data best (Table 2). Overall, lone wolves had a lower (but insignificant) tendency to travel northward than packs of wolves (Figure 3). Travel northward was more likely during dusk than day, though this relationship is also not significant. Lone wolves followed this pattern, and were most likely to travel north at dusk and south at dawn, however this crossing behavior was not significantly different than the likelihood to go north during the day. Finally, the likelihood of packs to travel north was not influenced by time of day or season (Supporting Information, Tables S4 and S5).

3.2 | Temporal trends in green bridge use by prey species and humans

Green bridge crossing by red deer, roe deer, wild boar and humans was best described by the global models, which included both time of day and season (Table 3). Similar to wolves, prey species had the lowest probability of crossing during the day in autumn (intercept; Figure 4). Red deer and wild boar crossed the green bridge significantly more during dawn, dusk and night than during the day. Roe deer crossed the green bridge most during dusk, whereas humans crossed the green bridge significantly less during dusk.

Seasonal use of the crossing structure differed between wolves, prey species and humans (Figure 4). Wolves crosses most in winter, roe deer and red deer activity peaked in spring, wild boar activity peaked in summer, and human activity peaked in autumn.

TABLE 1 AICc table of candidate models for the Poisson regression model describing the relationship between count of wolf crossings as a function of the season and period of the day (Crossing ~ Season + Period). Three outputs are presented: for the data reflecting overall count of wolf crossings, for the data reflecting the count of lone wolf crossings, and for the data reflecting count of wolf pack crossings

Model	AICc	ΔAICc	AICc weight
Overall count of wolf crossings			
Intercept + Time of day	349.8	0	0.631
Intercept + Time of day + Season	350.9	1.07	0.369
Intercept + Season	404	54.19	0
Null	414.7	64.83	0
Count of lone wolf crossings			
Intercept + Time of day	77.8	0	0.856
Null	82.5	4.72	0.081
Intercept + Season	83.6	5.77	0.048
Intercept + Time of day + Season	85.9	8.06	0.015
Count of wolfpack crossings			
Intercept + Time of day	88.2	0	0.668
Intercept + Time of day + Season	89.6	1.4	0.332
Intercept + Season	107.2	19.01	0
Null	112.8	24.62	0

Note: Top models are underlined.

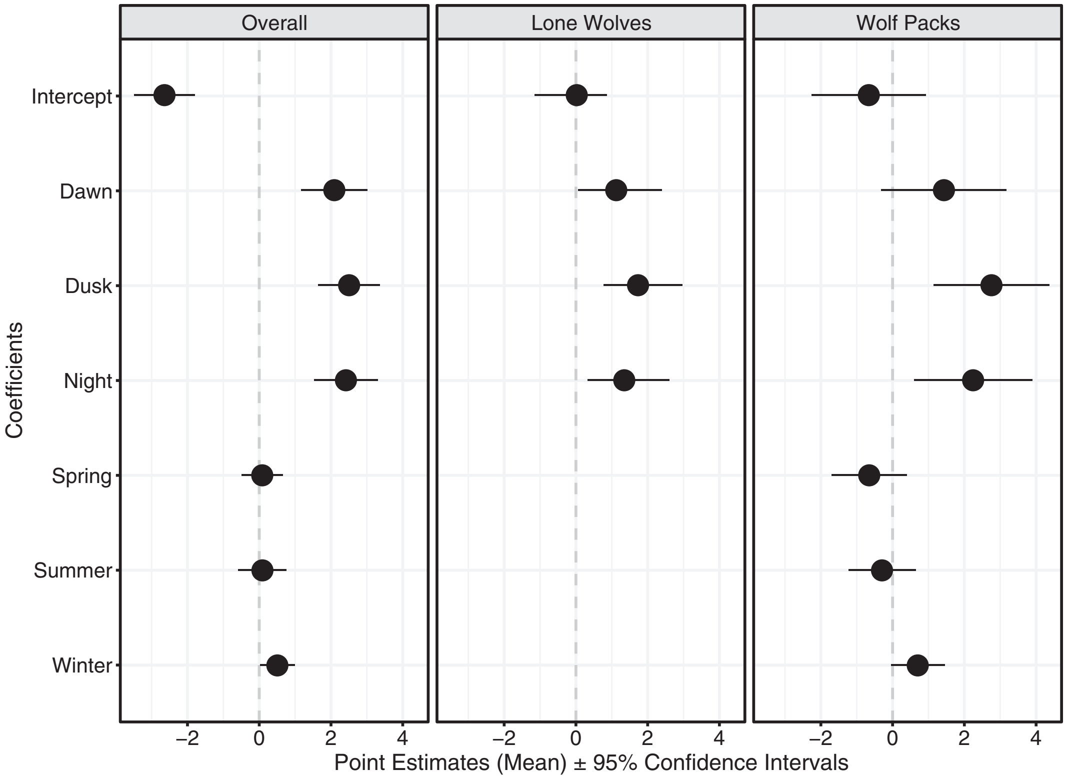

FIGURE 2 Estimated model coefficients (and 95% confidence intervals), for best candidate model(s) when evaluating the number of overall, lone and pack of wolves crossing the green bridge. Coefficients with estimates and 95% confidence intervals that do not overlap zero (vertical dotted line) are deemed significant predictors of crossing. Models reflect the results of the model selection process, and therefore overall crossing and crossings by packs were estimated as a function of season and time of day, whereas crossings by lone wolves was only estimated as a function of time of day. As such, the intercept for overall crossings and crossing by packs reflects autumn during the day, whereas the intercept for crossings by lone wolves reflects only day time crossing. *X*-axes vary to improve legibility

TABLE 2 AICc table of candidate models for the binomial regression model describing the likelihood that wolves crossed northward as a function of the season and period of the day (Northward Crossing ~ Season + Period). Three outputs are presented: for the data reflecting overall wolf crossings, for the data reflecting the lone wolf crossings, and for the data reflecting wolf pack crossings. The overall wolf crossing model had an additional explanatory variable for whether the event was of a lone wolf or a wolf pack

Model	AICc	ΔAICc	AICc weight
Overall probability of travelling north			
Intercept + Lone or Pack + Time of day	142.8	0	0.603
Intercept + Time of day	144.2	1.42	0.297
Intercept + Lone or Pack + Time of day + Season	147	4.29	0.071
Intercept + Time of day + Season	148.9	6.11	0.028
Null	155.9	13.16	0.001
Intercept + Lone or Pack	157.2	14.49	0
Intercept + Season	161.5	18.73	0
Intercept + Lone or Pack + Season	162.6	19.89	0
Probability of lone wolves travelling north			
Intercept + Time of day	90	0	0.901
Intercept + Time of day + Season	94.6	4.54	0.093
Null	100.1	10.09	0.006
Intercept + Season	106.1	16.1	0
Probability of wolf packs travelling north			
Null	57.2	0	0.698
Intercept + Time of day	59.2	2.04	0.252
Intercept + Season	62.8	5.6	0.043
Intercept + Time of day + Season	66.4	9.19	0.007

Note: Top models are underlined.

3.3 | Wolf-prey interactions

There were 134 wolf-prey interaction events. The majority of events occurred between wolves and red deer ($n = 102$; Supporting Information, Table S6). Wolf-roe deer ($n = 22$) and wolf-wild boar ($n = 10$) interactions were too infrequent to analyze rigorously. Events where red deer followed wolves were significantly shorter than events where wolves followed red deer ($p < .001$; wolf-before-red deer: average 613 min, range 2–5,651 min; wolf-after-red deer: average 852 min, range 1–11,333 min).

4 | DISCUSSION

Currently, there are seven green bridges across major highways throughout Brandenburg state, and the focal green bridge in this study is one of the most commonly used structures by wildlife. Wolves first crossed the investigated green bridge at the end of 2015, approximately 4 years after its construction, and they have used it annually since late 2017. Most other green bridges are used by wolves as well, especially during winter (LFE, 2019). Our study supports the myriad of others that show green bridges are used by wolves and prey species. Thus, green bridges could be a useful conservation tool to reduce the effects of habitat fragmentation and road mortality on wildlife, and may be helpful as wolves continue to recolonize their historic range (Bissonette & Adair, 2008; Clevenger & Waltho, 2005; Smith et al., 2015).

4.1 | Green bridge use by wolves, prey, and humans

Wolves showed distinct seasonal and daily patterns in their use of green bridges. Green bridge use was most frequently during winter, particularly by packs of wolves. Reduced spring and summer activity may be because wolves tend to utilize less of their territory during the reproductive period (Barja et al., 2005; Llaneza et al., 2014). Increased activity in the winter may be due to one or both packs south of the green bridge using the bridge within their hunting territory. As there was little seasonal effect of lone wolf crossing the green bridge, we were unable to support our prediction and demonstrate young individuals leaving the pack to search for their own territory (Mech & Boitani, 2003). This may still occur however we would need more data on lone crossings to be come to this conclusion.

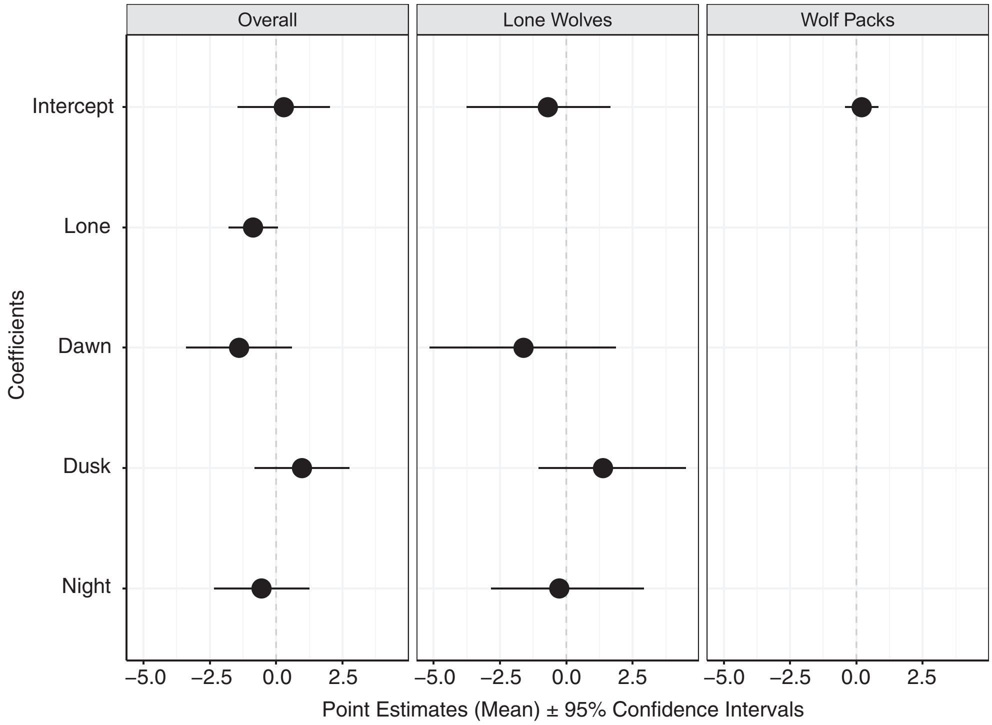

FIGURE 3 Estimated model coefficients (and 95% confidence intervals), for best candidate model when evaluating the probability of overall, lone and pack of wolves crossing the bridge towards the north. Coefficients with estimates and 95% confidence intervals that do not overlap zero (vertical dotted line) are deemed significant predictors of crossing. Models reflect the results of the model selection process, and therefore overall probability of crossing was estimated as a function of if the event was by a lone or pack of wolves and time of day, probability of lone wolves crossing was estimated as a function of time of day, and probability of packs of wolves crossing was only given an intercept. As such, the intercept for overall probability reflect crossing by packs during the day, and the intercept for lone wolves reflects the probability of crossing during the day. *X*-axes vary to improve legibility

Wolves displayed a tendency to travel northward more frequently during the day until dusk and southward more frequently at night until dawn—a pattern that was relatively consistent throughout the year. Given the little support for daily or seasonal patterns in packs, packs may on the one hand be expanding their territories, on the other hand lone wolves may be using the bridge for nightly hunting and exploration trips. Movement patterns are important to consider when deciding where to place green bridges in the landscape, as the surrounding landscape and resources available on either side of the road can heavily influence when and how often crossing structures are used (Bissonette & Adair, 2008; Clevenger & Waltho, 2005). In our study, we are unable to comment on how much the bridge helps in recolonization, however given the active northward movement it is possible that the wolves can find a path towards new territory using this green bridge.

Temporal patterns of predators and prey may reveal seasonal differentiation in green bridge use between predator and prey species. Red deer, roe deer and wild boar used the structure most often in spring, whereas wolf activity was low during this time. Unlike the variation between seasons, daily activity patterns for each species remained relatively consistent throughout the year. All species were most active during dawn and dusk and least active during the day. This was in contrast with human activity, which peaked during the daytime, but this difference may be a result of natural differences in diurnal activity patterns rather than a display of human avoidance. Since other studies suggest avoidance behavior in human species, especially wolves (Barrueto et al., 2014), studies on a smaller temporal scale are necessary to evaluate whether humans have an influence on wildlife use of crossing structures. However, with the evidence we can provide, we support our prediction that wolves are least active during the day on the green bridge.

While most wolf-prey interactions events were between wolves and red deer, none of these were direct interactions. Generally speaking, red deer followed wolves sooner than wolves followed red deer. This result suggests that there could be some interaction between red deer and wolves on the bridge, however the direction is unexpected, as the interactions favor red deer (Ford & Clevenger, 2010). This result supports other papers that

TABLE 3 AICc table of candidate models for the binomial regression model describing the likelihood that wolves crossed northward as a function of the season and period of the day (Northward Crossing ~ Season + Period). Three outputs are presented: for the data reflecting overall wolf crossings, for the data reflecting the lone wolf crossings, and for the data reflecting wolf pack crossings. The overall wolf crossing model had an additional explanatory variable for whether the event was of a lone wolf or a wolf pack

Model	AICc	ΔAICc	AICc weight
Red deer			
<u>Intercept + Time of day + Season</u>	<u>875.4</u>	<u>0</u>	<u>1</u>
Intercept + Season	1,006.8	131.41	0
Null	1,055.1	179.64	0
Intercept + Time of day	1,160.5	285.09	0
Roe deer			
<u>Intercept + Time of day + Season</u>	<u>415.1</u>	<u>0</u>	<u>0.94</u>
Intercept + Season	420.8	5.68	0.055
Intercept + Time of day	426	10.88	0.004
Null	428.8	13.71	0.001
Wild boar			
<u>Intercept + Time of day + Season</u>	<u>206.6</u>	<u>0</u>	<u>0.911</u>
Intercept + Time of day	211.3	4.66	0.089
Null	235.9	29.25	0
Intercept + Season	238.5	31.81	0
Humans			
<u>Intercept + Time of day + Season</u>	<u>176.9</u>	<u>0</u>	<u>0.93</u>
Intercept + Time of day	182.1	5.17	0.07
Intercept + Season	234.2	57.26	0
Null	244.4	67.45	0

Note: Top models are underlined.

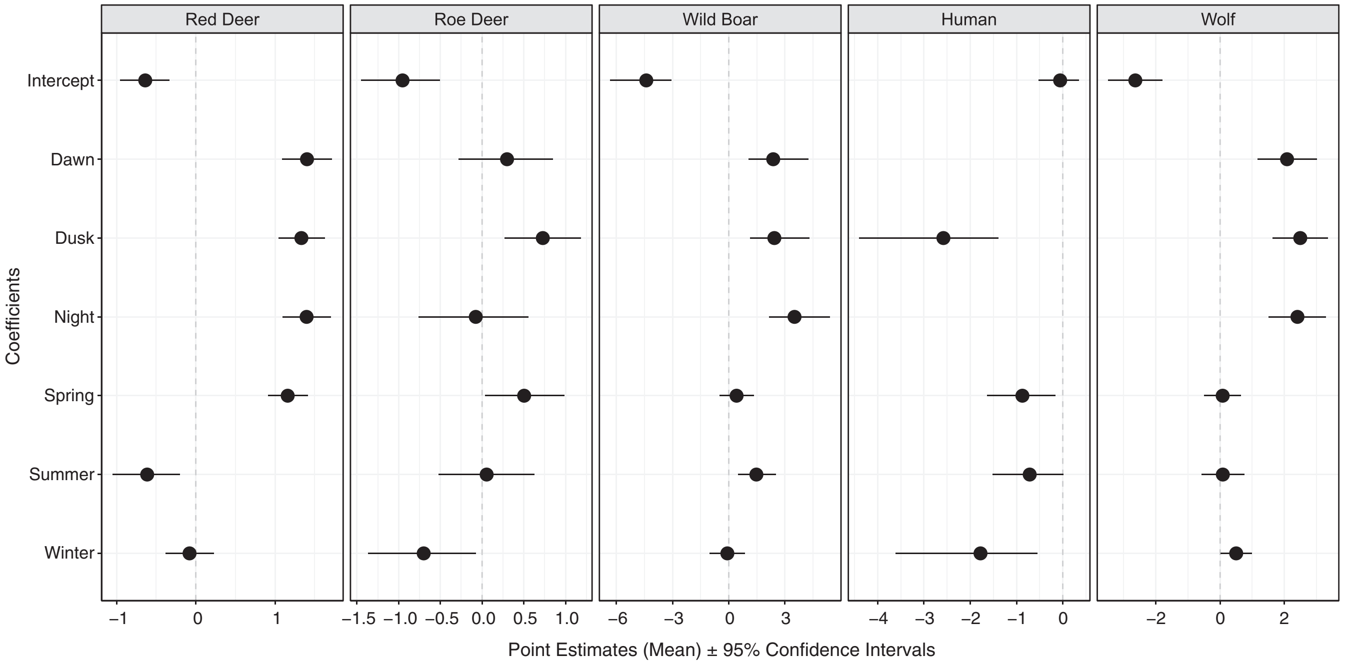

FIGURE 4 Estimated model coefficients (and 95% confidence intervals), for best candidate model(s) when evaluating the number of times red deer, roe deer, wild boar, humans and wolf (overall) cross the green bridge. Coefficients with estimates and 95% confidence intervals that do not overlap zero (vertical dotted line) are deemed significant predictors of crossing. Models reflect the results of the model selection process, and crossings were estimated as a function of season and time of day. The intercept for reflects crossing in autumn during the day. The human model does not include dawn or night so those variables are not estimated. Also, *x*-axes varied to improve legibility

show little or no evidence of prey-trapping at crossing structures (Ford & Clevenger, 2010, Mata, Herranz, & Malo, 2020, review: Little, Harcourt, & Clevenger, 2002). Since red deer comprise only approximately 3.6% of the wolf diet in Germany (Ansorge & Lippitsch, 2018), red deer may not actively avoid wolf presence. Roe deer and wild boar are preyed upon more frequently than red deer (Ansorge & Lippitsch, 2018), but interaction events were too few to evaluate statistically. We therefore cannot confirm or reject our hypothesis that roe deer and wild boar avoid crossing structures when the risk of predation is high.

4.2 | Using green bridges to reduce the impacts of roads on wolves

Wolf-vehicle collisions in Germany usually peak in February and November and reach their lowest levels in July and August (DBBW, 2020b; Supporting Information, Figure S1). Seasonal peaks in road-associated mortality coincide with peaks on the monitored green bridge, suggesting that increased movement by wolves at winter increases their risk of road-associated mortality. Pups are particularly in danger of being killed by vehicle collisions; they account for approximately 47% of the total wolf road-associated mortality (DBBW, 2020b). The increased risk of collisions may coincide with the migration period when young wolves disperse to search for territory; it is possible they are unaware of the dangers of traffic (Mech & Boitani, 2003). In these situations, green bridges may provide aid, as they have been shown to reduce road-associated mortality, especially when combined with fencing (Rytwinski et al., 2016), which is the standard in Brandenburg when building green bridges (BAST, 2014). As we have shown in our study, green bridges are used by predator and prey, and may provide means for multiple species to safely cross roads and expand their range.

4.3 | Future considerations

Green bridges can facilitate monitoring because of their relatively narrow design. For animals with wide home ranges, such as wolves, observation of these narrow paths with wildlife cameras provides an effective approach, especially for long-term monitoring (Ford, Clevenger, & Bennett, 2009; Šver et al., 2016). However, these cameras do have limitations; for example, they cannot detect fast-moving animals with absolute accuracy, resulting in underrepresentation of some fast-moving species, such as roe deer (Gužvica et al., 2014). We were also unable to identify and differentiate individuals with camera trapping. Therefore, our results regarding activity cannot differentiate between lone wolves that crossed the bridge only once (i.e., passing through on their way to their new territory) or those that crossed regularly (i.e., individuals from a pack on hunting missions). Future studies should consider these limitations when planning their sampling design.

To further understand the effectiveness of crossing structures in aiding dispersal and recolonization of wolves, additional analysis would be necessary to complement the camera-data collected in this study. For example, in this region, there are two known wolf packs whose territories overlap with the crossing structure (DBBW, 2020a). However, without genetic analysis (e.g., from fecal samples), we cannot determine whether one pack is using the structure more than the other, nor can be monitor how many wolves cross northwards over the green bridge and establish their own territory further north. Finally, the effectiveness of crossing structures cannot be evaluated through their apparent use, as presented in this study. Instead, effectiveness is better evaluated through a quantified reduction in mortality or barrier effects, for example comparing mortality on the roads before and after structure construction, or by using GPS-collaring to explore the role the green bridge may have in facilitating movement into new territories.

5 | CONCLUSION

The recent return of gray wolves to Germany can largely be attributed to the successful implementation of European and national conservation laws (Kiffner, Chapron, & König, 2019), with similar recovery trends among large carnivores in other European countries (Chapron et al., 2014). Green bridges can aid in conservation efforts, as they mitigate the negative effects of roads on wildlife. Our study showed that a green bridge was utilized by a variety of species, including wolves, and that wolf presence did not seem to deter potential prey species (red deer, roe deer, wild boar) from frequently using the bridge. Green bridges can help restore connectivity in the landscape and foster the spread of wildlife through the landscape (Bissonette & Adair, 2008), providing an effective tool for conservation. Future investigations into the effectiveness of green bridges to reconnect landscapes and to reduce wildlife road-associated mortality will further improve our knowledge on how best to aid wildlife recolonization of their historic range in a landscape heavily dominated by human activity.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

The study design, preparation and realization (setting up and controlling wildlife cameras) as well as the interpretation and first analysis of the pictures was carried out by Mike Plaschke. The statistical data analysis was mainly carried out by Manisha Bhardwaj. Mike Plaschke and Manisha Bhardwaj developed the main idea of the paper and wrote large parts of the manuscript; they are joint lead authors. Kornelia Dobiáš provided data on the green bridge and other green bridges and on road mortality by wolves and gave general support with the study design and set-up. Hannes J. König, Adam T. Ford, and Elena Wenz contributed to specific parts of the manuscript and to general coherence by writing, data analysis, preparing figures and literature review.

DATA AVAILABILITY STATEMENT

All data are available at the request of either of the lead authors, M. Plaschke or M. Bhardwaj, who can be contacted directly via email.

ETHICS STATEMENT

This research did not use animals or human subjects and only reported results from photos. We therefore did not require an animal ethics approval for this work.

AUDIENCE

Those interested in understanding landscape fragmentation, as well as those striving to mitigate and manage the impacts of linear infrastructure on the movement of wildlife; conservation researchers, policy-makers, planners or conservation practitioners.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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