

# Black bear translocations in response to nuisance behaviour indicate increased effectiveness by translocation distance and landscape context

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## Abstract

**Context.** Translocation is a widely used non-lethal tool to mitigate human–wildlife conflicts, particularly for carnivores. Multiple intrinsic and extrinsic factors may influence translocation success, yet the influence of release-site landscape context on the success of translocations of wildlife involved in nuisance behaviour is poorly understood. Moreover, few studies of translocated wildlife involved in nuisance behaviour have provided estimates of translocation success under different scenarios.

**Aims.** We evaluated the role of intrinsic (age, sex) and extrinsic (translocation distance, landscape composition) features on translocation success of American black bears (*Ursus americanus*) involved in nuisance behaviour and provide spatially explicit predictions of success under different scenarios.

**Methods.** We analysed data from 1462 translocations of 1293 bears in Wisconsin, USA, from 1979 to 2016 and evaluated two measures of translocation success: repeated nuisance behaviour and probability of returning to a previous capture location.

**Key results.** Translocation distances ranged from 2 to 235 km (mean = 57 km). Repeated nuisance behaviour was recorded following 13.2% of translocation events (192 of 1457) and was not significantly affected by translocation distance. Bears repeated nuisance behaviour and were recaptured at their previous captures site (i.e. returned) after 64% of translocation events (114 of 178). Return probability decreased with an increasing translocation distance, and yearling bears were less likely to return than were adults. The proportions of agriculture and forest within 75 km and 100 km respectively, of the release site had positive and negative effects on return probability.

**Conclusions.** Managers can use bear characteristics and landscape context to improve translocation success. For example, achieving a 10% predicted probability of return would require translocation distances of 49–60 km for yearlings in low-agriculture and high-forest landscapes. In contrast, estimated return probability for adults was  $\geq 38\%$  across all translocation distances (0–124 km) and almost all landscape contexts.

**Implications.** Our results emphasise the importance of considering the effects of landscape conditions for developing spatially explicit guidelines for maximising translocation success.

**Additional keywords:** agriculture, human–wildlife conflict, nuisance wildlife, *Ursus americanus*.

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## Introduction

Managing human–wildlife conflicts is an on-going concern in many areas because growing human populations result in increasing encounter rates with wildlife (Messmer 2000; Can *et al.* 2014). These conflicts often result in negative impacts to both humans (e.g. property damage, zoonotic diseases, livestock loss, personal injury or death) and wildlife (e.g. fitness costs, fear or mortality; Conover *et al.* 1995; Inskip and

Zimmermann 2009) and require substantial investments in time and resources from wildlife management agencies (Beringer *et al.* 2002; Spencer *et al.* 2007). Lethal control is applied in many human–wildlife conflicts (Baker and Harris 2006; Inskip and Zimmermann 2009), but sociological, ethical and conservation (e.g. endangered species) concerns have increased the demand for non-lethal alternatives (Fall and Jackson 2002).

Translocation (i.e. capturing an individual and transporting it to and releasing it at a different location within its geographic range) is a widespread non-lethal approach for managing nuisance wildlife behaviour (Fischer and Lindenmayer 2000; Massei *et al.* 2010). However, translocations are potentially stressful to the animals involved (Cromwell *et al.* 1999; Beringer *et al.* 2002) and may lead to increased mortality (Reinert and Rupert 1999; Beringer *et al.* 2002). Moreover, translocations are often financially and logistically costly to implement (Riley *et al.* 1994) and may vary in their effectiveness of mitigating nuisance behaviour (Rogers 1986; Linnell *et al.* 1997). Understanding the conditions under which translocation mitigates nuisance behaviour is important for increasing translocation efficiency and efficacy. Previous studies across multiple terrestrial vertebrate taxa have found relationships between intrinsic factors, such as age or sex (Moehrenschlager and Macdonald 2003; Pinter-Wollman *et al.* 2009; Bauder *et al.* 2014; Gedir *et al.* 2018), and extrinsic factors, such as release method or habitat features (Tuberville *et al.* 2005; Moorhouse *et al.* 2009; Devineau *et al.* 2011; McCoy *et al.* 2014), and various post-translocation behaviours. Incorporating such factors into analyses examining post-translocation nuisance behaviour could be used to predict the absence of such behaviours (i.e. translocation success) as a function of those factors. However, the effects of release-site environment on nuisance wildlife translocation success have received less focus than have conservation-based translocations (Linnell *et al.* 1997; cf. Jarvie *et al.* 2014; Stone and Guy 2017) and few nuisance wildlife studies have provided model-based predictions of translocation success under different spatially explicit scenarios (Landriault *et al.* 2009).

Conflict management between humans and American black bears (*Ursus americanus*) involves substantial effort from wildlife management agencies (Spencer *et al.* 2007) and translocation is widely used to mitigate human–bear conflicts (Rogers 1986; Linnell *et al.* 1997). Previous studies of translocated black bear involved in nuisance behaviour have defined translocation success as an absence of repeated nuisance behaviour or as a translocated bear not returning to its previous capture area (Linnell *et al.* 1997; Landriault *et al.* 2009). Either measure of success may vary across sites and studies (Landriault *et al.* 2009; Shivik *et al.* 2011; Lewis *et al.* 2019); yet, most previous studies of bear translocation have focussed on the probability of the bear returning to the previous capture area. These studies have found that a bear's age, sex and translocation distance may all influence its probability of returning (Rogers 1986; Fies *et al.* 1987; Landriault *et al.* 2009; Alldredge *et al.* 2015). However, less is known about factors that influence the probability of repeated nuisance behaviour. Moreover, relatively little is known about how the post-release behaviour of translocated bears is affected by the habitat characteristics or the landscape context of the release site compared with the effects of age, sex, or translocation distance. McArthur (1981) found that translocation success for black bears involved in nuisance behaviour increased with an increasing topographic relief and elevation gain between capture and release sites. Both natural and anthropogenic land covers can restrict or facilitate black bear movements (Karelus *et al.* 2017; Dittmer *et al.* 2018), which, in turn, may affect the ability or inclination of translocated individuals to return.

Beginning in 1979, the Wisconsin Department of Natural Resources (WDNR) and United States Department of Agriculture's Animal Plant Health Inspection Service (APHIS) have managed a black bear nuisance abatement program. Complaints have been resolved by providing technical assistance and advice (Voyles *et al.* 2015), with translocation generally reserved for bears deemed to have a high probability of repeating the nuisance behaviour (e.g. Shivik *et al.* 2011). The black bear population in Wisconsin has increased to over 20 000 individuals (Allen *et al.* 2018), which has coincided with a range expansion into central and southern Wisconsin, an area with higher human populations and agricultural activity (Malcolm and Van Deelen 2010). This may bring bears into an increasing conflict with humans, making it important to both understand the efficacy of the Wisconsin bear translocation program and provide guidelines for maximising the program's efficiency and efficacy.

We used a long-term dataset (1979–2016) of black bear captures and translocations in Wisconsin to address three objectives. First, we compared two definitions of translocation success, namely (1) an absence of repeated nuisance behaviour, and (2) an absence of repeated nuisance behaviour within the bear's original home range (i.e. a bear not returning to its capture area). Second, we evaluated how translocation success is influenced by multiple intrinsic (age, sex) and extrinsic (translocation distance, landscape composition) factors. Third, we used the results of our analyses to provide model-based predictions of translocation success under different spatially explicit scenarios.

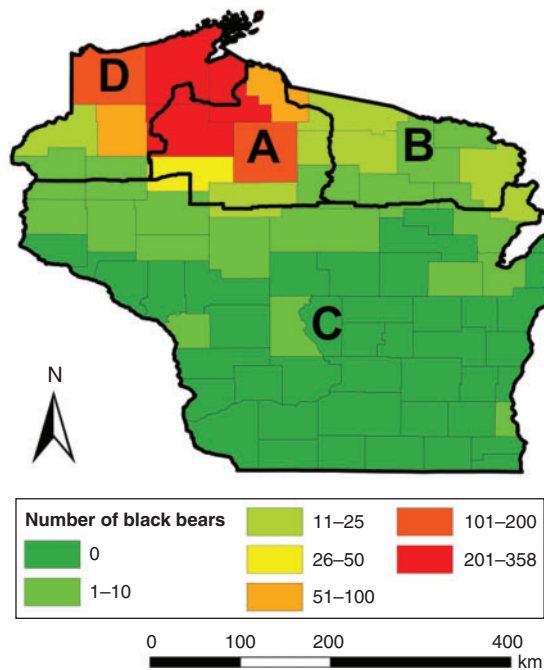
## Methods

### Study area

The WDNR manages black bear populations in four distinct zones with unique quotas and hunting regulations (Allen *et al.* 2018). Most of the bear population resides in the northern half of Wisconsin (Management zones A, B and D, Fig. 1). These zones cover ~84 000 km<sup>2</sup> north of where southern broadleaf forest transitions to northern mixed broadleaf–conifer forest (Curtis 1959). The most common habitat in this region is maple–basswood forest, including sugar maple (*Acer saccharum*), northern red oak (*Quercus rubra*), American beech (*Fagus grandifolia*) and eastern hemlock (*Tsuga canadensis*; Curtis 1959). Mean monthly temperature and precipitation during 1979–2016 ranged from –10°C to 21°C and from 3 to 11 cm respectively. Seasonal snowfall ranged from 68 to 204 cm (all weather data are available at <http://www.aos.wisc.edu/~sco/clim-history/state/index.html#Variable>, accessed 26 February 2020).

### Black bear captures and translocation

Black bears in the present study were captured from 1979 to 2016, primarily by WDNR staff led by B. Kohn from 1979 to 1989, and under a cooperative agreement with APHIS from 1990 to 2016. Reports of bear nuisance behaviour were classified as either nuisance reports (problematic bear behaviour, damage to bird feeders, garbage cans, gardens, bears present in urban environments, or campgrounds), agricultural-damage reports (primarily corn, but also other agriculture and bee hives) or property-damage reports (Willing and Kohn 1992).



**Fig. 1.** Number of translocated black bear captures by county and management zone (denoted by letters) in Wisconsin from 1975 to 2016.

The type of nuisance activity associated with each translocation was not recorded but most translocations of marked bears annually were in response to nuisance- and property-damage reports (e.g. Engstrom *et al.* 2015). Agency personnel first attempted to resolve all complaints over the phone, but attempted to capture and translocate bears when deemed necessary.

Our data consisted of 1916 translocation events from 1659 bears marked with unique ear tags, lip tattoos, or both. We used 1462 events from 1293 marked and translocated individuals for which capture and release location data were available. Sample sizes for subsequent analyses varied depending on the completeness of the data for any given analysis (see below). Bears designated for translocation were primarily captured using culvert traps ( $n_{\text{culvert trap}} = 918$ ,  $n_{\text{cage trap}} = 2$ ,  $n_{\text{unrecorded}} = 542$ ), and immobilised using chemical immobilisation (Shivik *et al.* 2011; Kreeger and Arnemo 2012). Each bear was classified as a yearling or adult ( $\geq 2$  years) and sexed before release. All bears were hard released and all capture, handling and release procedures were consistent with the American Society of Mammologist's Guidelines for Use of Wild Mammals in Research and Education (Sikes *et al.* 2016). Personnel also recorded whether a bear was harvested through hunting or died of other causes (e.g. road mortality) and we considered all mortalities as dead recoveries. All live recaptures were made in association with nuisance behaviour and we, therefore, consider recaptures as indicative of repeated nuisance behaviour.

#### Translocation and return distances

Capture and release locations were recorded to the nearest section using the public-land survey system (PLSS), which we converted to geographic coordinates using a shapefile of Wisconsin townships–ranges–sections ([https://navigator.blm.](https://navigator.blm.gov/api/share/5ff91e1972c9ac84)

[gov/api/share/5ff91e1972c9ac84](https://navigator.blm.gov/api/share/5ff91e1972c9ac84), accessed 9 November 2018). We used only records including the township, range, range direction, and section (median polygon size = 0.91 km) or, in a minority of cases (<1%), the township, range and range direction (median polygon size = 5.44 km). We measured the distance between capture and release locations as a translocation distance.

We followed the approach of previous studies of black bear translocations and considered a bear to have returned if it was recaptured within a distance approximating the diameter of a home range (Fies *et al.* 1987; Landriault *et al.* 2009; Alldredge *et al.* 2015). Because male black bears typically have larger home ranges than do females (Alt *et al.* 1980; Garshelis and Pelton 1981), we used separate diameters for each sex. We performed a systematic review of all published home-range estimates for black bears in habitats similar to that of bears in northern Wisconsin (the northern mixed-forest ecotone), following the methods of Allen *et al.* (2018). We tabulated the maximum home-range sizes (Table S1, available as Supplementary material to this paper) after excluding outliers noted by authors. We converted the reviewed home-range sizes to diameters by assuming circular home ranges and calculated the mean diameter across studies by sex (8 km for females and 13 km for males). We used maximum, rather than mean, home-range sizes, because our method for estimating home-range diameter may underestimate the diameter of elongate home ranges. However, our mean diameters corresponded to breaks in the distribution distances between release locations and subsequent capture locations for bears in our study (Fig. S1, available as Supplementary material to this paper).

#### Land cover

We used the National Land Cover Data (NLCD) from 2001, 2006 and 2011 ([www.mrlc.gov](http://www.mrlc.gov), accessed 13 December 2018), and re-projected to WGS84 in ArcMap ver. 10.6, ESRI, Inc. (2017) to quantify release-site landscape composition. We measured the proportion of urban (NLCD Classes 21, 22, 23 and 24), agriculture (81 and 82), forest (41, 42, and 43) and wetland (90 and 95) land covers within circular buffers around each bear's release location with the *extract* function in the package RASTER (Hijmans 2018) in Program R (ver. 5.5.1, R Core Team 2018). We excluded open water before calculating proportions. Because animals may respond differently to landscape features at varied spatial scales (Thompson and McGarigal 2002; Bowyer and Kie 2006), we used a range of buffer sizes (10-, 20-, 30-, 50-, 75- and 100-km radii) to measure landscape composition at scales ranging from immediately around the release site up to the entire potential return route.

#### Statistical analyses

We conducted all analyses in Program R. We used chi-square goodness-of-fit tests to test for equal proportions of captures between sexes and age classes.

To test for effects on the probability of recapture following a translocation (i.e. probability of repeated nuisance behaviour) while accounting for both the high proportion of bears with single records and the non-independence of multiple records from the same bear, we used a bootstrapping approach combined

with generalised linear models (GLM) with binomial error distributions and logit links. We first randomly subsampled 75% of all translocation events, while ensuring that only a single event was randomly selected from bears with multiple events. We then fit the binomial GLM and recorded the  $\beta$  estimate for the independent variable and the predicted probabilities of recapture. We repeated this process 10 000 times, and report the 2.5th, 50th and 97.5th quantiles (i.e. median and 95% CI) of the betas and predicted probabilities. We drew inference from effects whose 95% CI did not include zero. We tested for effects of sex, age, translocation distance, whether or not the translocation was a bear's first translocation or a subsequent translocation (e.g. second or third translocation), and whether or not a bear was eventually recovered dead at any point following its first translocation.

We evaluated the effects of age, sex and translocation distance on the probability of returning using generalised linear mixed models (GLMM) with binomial error distributions and the logit link with random intercepts for individuals. All bears used in these analyses repeated nuisance behaviour after their first translocation; so, the probability of returning is synonymous with the probability of repeating nuisance behaviour within a bear's original home range. To minimise the effects of location error and within-home range familiarity, we removed translocations less than our home-range diameters (e.g. Landriault *et al.* 2009). Because bears translocated further generally have lower return probabilities (Rogers 1986; Landriault *et al.* 2009), we retained translocation distance in each model and tested for additive and interactive effects of distance with sex and age. We fit all GLMM using LME4 (Bates *et al.* 2015, 2019) and  $z$ -score standardised translocation distance to facilitate model convergence. We ranked candidate models using Akaike's information criterion adjusted for small sample sizes ( $AIC_c$ ; Burnham and Anderson 2002) and calculated  $AIC_c$  weights ( $w$ ) and evidence ratios for each model. We calculated model-averaged  $\beta$  estimates and 95% CI across models containing a given covariate (Grueber *et al.* 2011) and drew inferences from effects whose model-averaged 95% CI did not include zero.

To evaluate the effect of release-site landscape composition on return probability, we first identified the characteristic scale (i.e. the scale with the lowest  $AIC_c$ ; Holland *et al.* 2004) for each land-cover covariate individually. We added land cover to the best supported model from the previous analysis, to test our prediction that land cover would explain additional variation in return probability. For our land-cover analyses, we discarded all entries before 1995 (corresponding to a resumption of marking bears after cessation from 1991 to 1994, Fig. S2) to minimise the time lag between the date of translocation and the date of our earliest land-cover data (2001). We assigned land-cover data to the remaining entries by using the NLCD data whose year was closest to the capture year of each entry. We evaluated a single model for each land-cover covariate because of limited sample sizes and high collinearity between forest and agriculture ( $r = -0.78$ ). We  $z$ -score-standardised continuous covariates and visualised effect sizes for age, sex and translocation distance by using model-averaged predicted values across all land-cover models. Because we observed support for interactive effects of age and translocation distance, we conducted a *post hoc* analysis where we fit four additional land-cover models, each including an interaction between age and land cover. We drew inference from

these *post hoc* land-cover models only if they received greater empirical support than their corresponding additive model.

To estimate translocation success under different spatially explicit scenarios, we calculated the translocation distances required to achieve a predicted probability of 0.10, 0.25, 0.38 (for comparison with Landriault *et al.* 2009) and 0.50 of returning for different age–sex combinations. We note that these guidelines apply to bears that resumed nuisance behaviour (i.e. were recaptured following translocation). Because only two land-cover covariates (forest and agriculture) had greater empirical support than did our null model (containing only age, sex, and translocation distance), we calculated model-averaged predicted probabilities across all models (additive and interactive) containing these covariates and the null model. We visually examined the bivariate distribution of the percentages of agriculture and forest land-cover values at their characteristic scales across all release locations and selected the following five combinations spanning the domain of our data at which to estimate predicted probabilities of return (land-cover percentages reported in parentheses): high agriculture (12%) and low forest (52%), medium agriculture (7%) and low forest (52%), medium agriculture (7%) and medium forest (59%), low agriculture (4%) and medium forest (59%), and low agriculture (4%) and high forest (64%). Finally, we predicted the return probabilities at all observed release locations used in the land-cover analyses for each age–sex combination.

## Results

### *Bear demography and spatial distribution*

Significantly ( $P < 0.0001$ ) more males ( $n = 872$ , 70%) than females ( $n = 382$ , 30%) were caught and translocated. Significantly ( $P < 0.0001$ ) more adults ( $n = 830$ ) than yearlings ( $n = 225$ ) were caught and translocated. There was no significant ( $P = 0.29$ ) difference in the proportion of males and females captured in each age class. Most (92%) incidents that led to translocation were in Zones A and D ( $n_A = 762$ ,  $n_D = 576$ ) with smaller numbers in Zones B and C ( $n_B = 77$ ,  $n_C = 34$ ). Five counties had  $>100$  captures (Fig. 1), including Sawyer ( $n = 358$ ), Ashland ( $n = 239$ ), Bayfield ( $n = 214$ ), Price ( $n = 176$ ), and Douglas ( $n = 157$ ).

### *Bear translocations and repeated nuisance behaviour*

Mean translocation distance across 1449 translocations (1282 bears) was 57 km (s.d. = 22 km, range 2–235; Fig. S3). Translocated bears were not recaptured following the majority (86.8%) of translocation events ( $n = 1457$ ) and most translocated bears ( $n = 1289$ ) were not recaptured after their first translocation event (87.7%). Of 197 recaptures of translocated bears, most of these recaptures were a bear's first recapture ( $n = 161$ , 82%), although three recaptures were the fourth recapture for those bears ( $n = 3$ , 0.2%). Most translocated bears that were recovered dead ( $n = 490$ , 38.0%) were harvested ( $n = 463$ , 94.5%), followed by vehicle mortalities ( $n = 24$ , 4.9%) and other mortality sources ( $n = 3$ , 0.6%). The percentage of translocated bears that were not recovered dead ( $n = 799$ ) and that were never recaptured was 86%.

After evaluating factors influencing the probability of being recaptured following a translocation (i.e. repeated nuisance

**Table 1.** Candidate model rankings based on Akaike's information criterion adjusted for small sample sizes ( $AIC_c$ ) for the effects of translocation distance (DST), age (AGE; yearling, adult) and sex (SEX) on the probability of returning by translocated black bears, with random intercepts for individuals, excluding one observation of an adult male not returning after being translocated 165 km  
w,  $AIC_c$  weight

Parameter	K	Log-likelihood	$AIC_c$	$\Delta AIC_c$	w	Cumulative w	Evidence ratio
SEX + AGE × DST	6	-74.85	162.33	0.00	0.47	0.47	1.00
SEX + AGE + DST	5	-76.53	163.52	1.18	0.26	0.73	1.81
AGE	4	-78.12	164.53	2.20	0.16	0.88	3.00
AGE + SEX × DST	6	-76.23	165.09	2.76	0.12	1.00	3.97
SEX	4	-85.72	179.74	17.40	0.00	1.00	6010.17
Null	2	-89.30	182.69	20.35	0.00	1.00	26 289.26
DST	3	-89.04	184.26	21.93	0.00	1.00	57 839.39

behaviour), we found that only two covariates had coefficient estimates whose 95% CI did not include zero. Translocated bears were less likely to be recaptured following their first translocation (0.07, 95% CI = 0.05–0.08) than any subsequent translocation (i.e. their second, third, or fourth translocation; 0.14, 95% CI = 0.07–0.21) ( $\beta = 0.81$ , 95% CI = 0.05–1.36). Translocated bears that were eventually recovered dead (0.05, 95% CI = 0.04–0.07) were also less likely to be recaptured before being recovered dead than were translocated bears that were never recovered dead (0.08, 95% CI = 0.06–0.10;  $\beta = -0.46$ , 95% CI = -0.93 to -0.06). While males had a lower recapture probability than did females (males: 0.07, 95% CI = 0.05 to 0.08; females: 0.09, 95% CI = 0.06 to 0.11), the 95% CI overlapped zero ( $\beta = -0.29$ , 95% CI = 0.69 to -0.14). Adults had a higher recapture probability than did yearlings (adults: 0.08, 95% CI = 0.06 to 0.09; yearlings: 0.06, 95% CI = 0.03 to 0.08), but the 95% CI overlapped zero ( $\beta = -0.34$ , 95% CI = -0.97 to 0.13). The effect of translocation distance was negative, but the 95% CI also overlapped zero ( $\beta = -0.09$ , 95% CI = -0.31 to 0.10) and the predicted recapture probabilities at the minimum, mean and maximum observed translocation distances (3, 57 and 235 km respectively) were 0.09 (95% CI = 0.05 to 0.14), 0.07 (95% CI = 0.06 to 0.08) and 0.04 (95% CI = 0.01 to 0.14) respectively.

#### Probability of repeated nuisance behaviour around the capture site

We examined the 178 translocation events from 147 bears ( $n_{\text{males}} = 103$ ,  $n_{\text{females}} = 72$ ;  $n_{\text{adults}} = 119$ ,  $n_{\text{yearlings}} = 23$ ) that were followed by repeated nuisance behaviour (i.e. recaptured) and had sufficient data with which to determine post-release movements. Most of these translocation events were a bear's first translocation ( $n = 124$ , 84%), but 17 events were a bear's second translocation (12%), four were a bear's third translocation (3%) and two were a bear's fourth translocation (1%). Median translocation distance for these 178 translocations was 53 km (IQR = 41–66 km, range = 19 to 167 km). Bears returned to their capture area and repeated nuisance behaviour (i.e. returned) following 64% ( $n = 114$ ) of these translocation events.

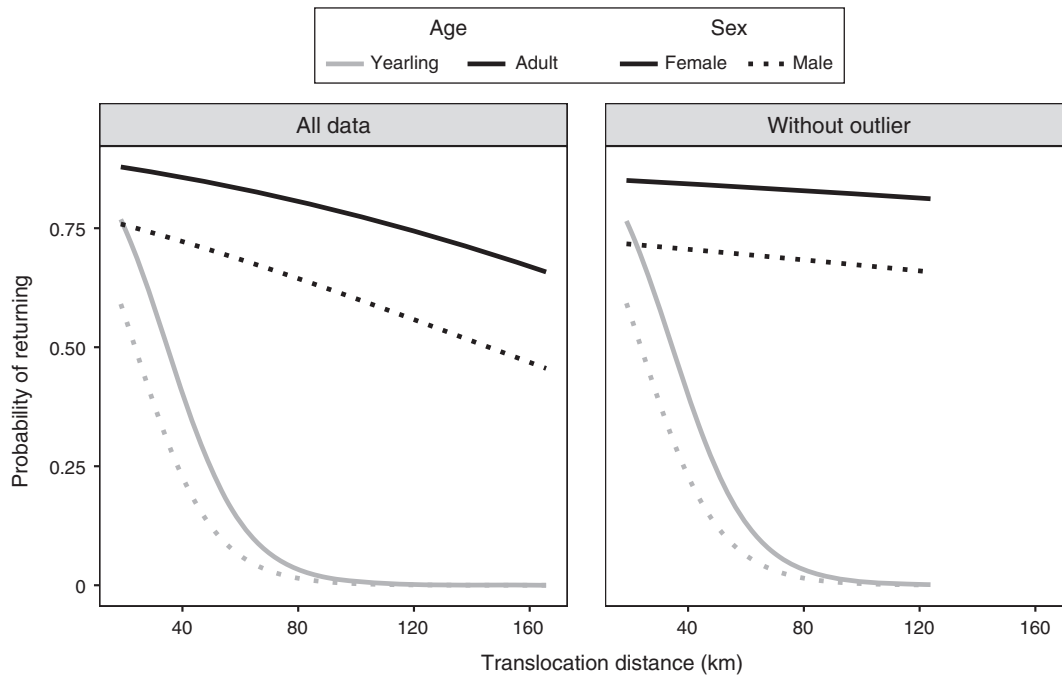
We had 138 translocation events from 115 bears with sufficient data to evaluate the effects of sex, age, and translocation distance on return probability. One 165-km translocation of an adult male that was not recaptured within its original home range was an outlier relative to other translocated adults (see below);

so, we report results without this translocation event (for results including this translocation event, see Tables S2 and S3). Four models had 100% of the cumulative  $AIC_c$  weight and all contained age (Table 1). The top-ranked model included an interactive effect of age and translocation distance and had 1.81 times the empirical support of the model with an additive effect of age and translocation distance. The model-averaged 95% CI for the main effect for age excluded zero and indicated that juveniles had lower return probabilities than did adults ( $\beta = -2.74$ , 95% CI = -4.78 to -0.70), whereas the model-averaged 95% CI for the main effect of sex included zero ( $\beta = -0.79$ , 95% CI = -1.65 to 0.07). The coefficient estimate for the interactive effect between age and translocation distance was almost identical regardless of whether the outlying observation was excluded (excluded:  $\beta = -1.40$ , 95% CI = -3.27 to 0.46; included:  $\beta = -1.41$ , 95% CI = -3.41 to 0.60). Return probability decreased with an increasing translocation distance for juveniles (Fig. 2). However, removing the outlying observation virtually removed any relationship between return probability and translocation distance for adults (Fig. 2).

#### Effect of landscape composition on probability of returning

We had 106 translocation events (excluding the potential outlier described above) from 87 bears with sufficient data to evaluate the effects of land cover on return probability. Urban landscape had the strongest effect at the 10-km scale, agriculture had the strongest effect on return probability at the 75-km scale, and forest and wetland had the strongest effect at the 100-km scale (Fig. S4). The means and ranges of the percentages of each land cover within the buffer at their characteristic scales were 7.6% (3.0 to 26.8%) for agriculture, 58.8% (47.3 to 64.6%) for forest, 21.9% (14.1 to 29.6%) for wetland, and 0.003% (0.0 to 0.01%) for urban landscape.

Adding agriculture or forest to the top-ranked model with only age, sex and translocation distance resulted in 4.9 and 2.3 times more support respectively, relative to the model with only age, sex and translocation (Table 2). Return probability increased and decreased with increasing amounts of agriculture and forest respectively (Fig. 3). These results were similar when including the aforementioned outlier (Table S3). The *post hoc* model including an interaction between agriculture and age had 1.1 times the empirical support of the model including an additive effect of agriculture and age ( $w = 0.43$  and 0.38 respectively) and 14.9 and 13.1 times the empirical support



**Fig. 2.** Probability of returning for translocated black bears by sex and age classes at the time of capture as a function of translocation distance with ( $n = 107$ ) and without ( $n = 106$ ) one observation of an adult male not returning after being translocated 165 km. Predicted values were model-averaged across all additive and interactive land-cover models, with land-cover covariates being held constant at their mean values.

**Table 2.** Candidate model rankings for the effects of translocation distance, age (yearling, adult), sex and land-cover covariates on the probability of returning by translocated black bears excluding one observation of an adult male not returning after being translocated 165 km

Each land-cover covariate was included at its characteristic scale (10 km for urban, 75 km for agriculture, 100 km for forest and wetland) and the null model includes only non-land-cover covariates. The evidence ratio indicates the support of Model  $i$  relative to the null model.  $\beta$ , the fixed-effect parameter estimate with its 95% CI;  $w$ ,  $AIC_c$  weight

Parameter	$K$	Log-likelihood	$AIC_c$	$\Delta AIC_c$	$w$	Cumulative $w$	Evidence ratio	$\beta$	Lower 95% CI	Upper 95% CI
AGRICULTURE + SEX + AGE $\times$ DST	7	-51.72	118.59	0.00	0.76	0.76	14.93	1.00	0.15	1.86
FOREST + SEX + AGE $\times$ DST	7	-53.61	122.36	3.77	0.11	0.87	2.27	-0.53	-1.10	0.03
SEX + AGE $\times$ DST	6	-55.57	124.00	5.41	0.05	0.92	1.00	-	-	-
WETLAND + SEX + AGE $\times$ DST	7	-54.53	124.20	5.61	0.05	0.97	0.90	-0.37	-0.89	0.14
URBAN + SEX + AGE $\times$ DST	7	-54.85	124.84	6.25	0.03	1.00	0.66	-0.26	-0.69	0.16

respectively, of the model with only age, sex and translocation ( $w = 0.03$ ). The *post hoc* model including an interaction between forest and age had less support than its corresponding additive model ( $w = 0.02$  and  $0.07$  respectively).

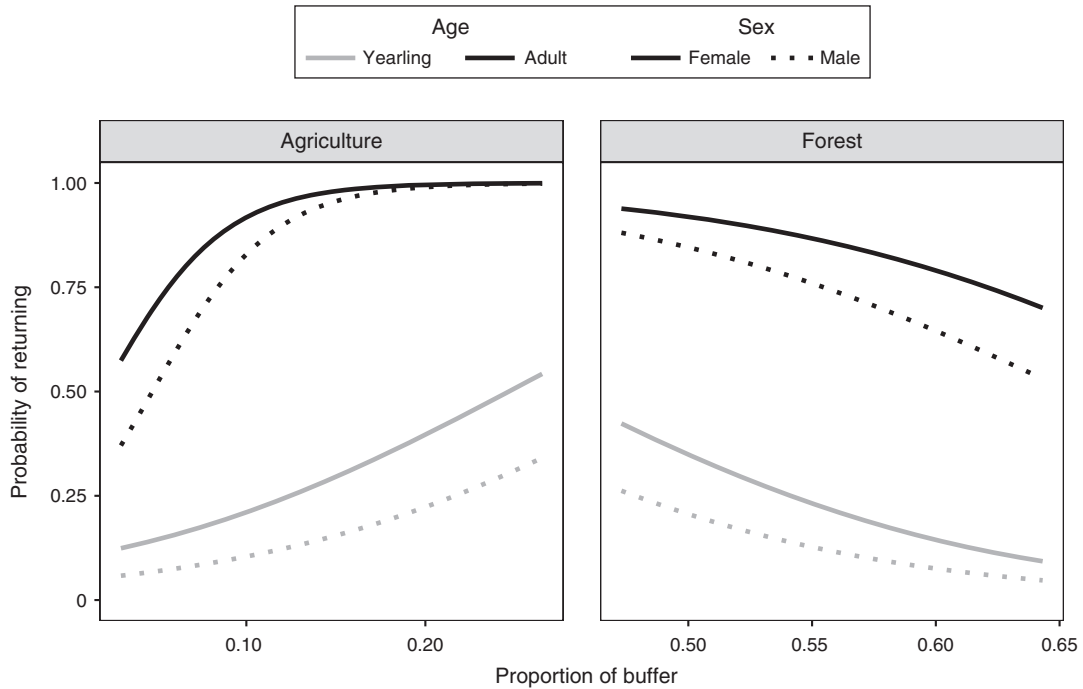
*Guidelines for translocation distances to minimise repeat nuisance behaviour*

The model-averaged predicted return probabilities indicated that the translocation distance needed to achieve a specified probability of returning varied widely by age class (Table 3). Yearlings needed to be translocated the shortest distances and had a 0.10 probability of returning when translocated  $\geq 49$ –60 km, depending on sex and landscape context. In contrast, predicted returning probabilities for adults did not fall

below 0.38 for any of the landscape contexts we evaluated across nearly the entire range of translocation distances used in our analyses (up to 124 km). Predicting return probabilities across actual release sites used in our landscape-composition analyses indicated that return probability was lowest in the northern regions of Zones A and D (Fig. S5).

**Discussion**

We found that our definition of translocation success strongly influenced the apparent success of translocation in mitigating human–black bear conflicts in Wisconsin. Translocated black bears in our study were recaptured resuming nuisance behaviour following 13.2% of translocation events, suggesting that translocation acts as a strong deterrent to repeated nuisance behaviour



**Fig. 3.** Model-averaged predicted probabilities of returning by translocated black bears as a function of the proportion of agriculture and forest land cover within 75 km and 100 km respectively, of a bear’s release point, excluding one observation of an adult male not returning after being translocated 165 km. Results were virtually identical when this individual was included. Predictions were averaged across the two models (additive and interactive) containing each land cover and the null model containing only age, sex and translocation distance (held constant at its mean value).

**Table 3. Minimum translocation distances (km) needed to reach a certain probability of returning for translocated black bears, excluding one observation of an adult male not returning after being translocated 165 km**

Probabilities represent the model-averaged predicted probabilities of returning across all additive and interactive models with agriculture (Ag.) or forest and a null model with only age, sex and translocation distance. Percentages of agriculture and forest are the percentages of each land cover within 75-km- and 100-km-radius buffers respectively, at the 5th (L), 50th (M) and 95th (H) quantiles. Values of ‘>124’ mean that model-averaged predicted probabilities did not fall below the specified threshold across the range of translocation distances used in the analyses (max. = 124 km)

Sex	Age	Agriculture	Forest	0.10	0.25	0.38	0.50
Male	Yearling	H Ag. (12%)	L Forest (52%)	60	45	37	30
Male	Yearling	L Ag. (4%)	H Forest (64%)	49	34	26	19
Male	Yearling	L Ag. (4%)	M Forest (59%)	49	35	26	20
Male	Yearling	M Ag. (7%)	L Forest (52%)	54	39	31	24
Male	Yearling	M Ag. (7%)	M Forest (59%)	52	37	29	23
Male	Adult	H Ag. (12%)	L Forest (52%)	>124	>124	>124	>124
Male	Adult	L Ag. (4%)	H Forest (64%)	>124	>124	>124	19
Male	Adult	L Ag. (4%)	M Forest (59%)	>124	>124	>124	27
Male	Adult	M Ag. (7%)	L Forest (52%)	>124	>124	>124	>124
Male	Adult	M Ag. (7%)	M Forest (59%)	>124	>124	>124	>124
Female	Yearling	H Ag. (12%)	L Forest (52%)	71	56	48	41
Female	Yearling	L Ag. (4%)	H Forest (64%)	60	45	37	30
Female	Yearling	L Ag. (4%)	M Forest (59%)	61	46	37	31
Female	Yearling	M Ag. (7%)	L Forest (52%)	65	50	42	35
Female	Yearling	M Ag. (7%)	M Forest (59%)	63	48	40	34
Female	Adult	H Ag. (12%)	L Forest (52%)	>124	>124	>124	>124
Female	Adult	L Ag. (4%)	H Forest (64%)	>124	>124	>124	>124
Female	Adult	L Ag. (4%)	M Forest (59%)	>124	>124	>124	>124
Female	Adult	M Ag. (7%)	L Forest (52%)	>124	>124	>124	>124
Female	Adult	M Ag. (7%)	M Forest (59%)	>124	>124	>124	>124

among black bears involved in nuisance behaviour in Wisconsin. This may be due to capture, immobilisation and transportation having deterrent effects (Clark *et al.* 2002). Lewis *et al.* (2019), Landriault *et al.* (2009) and Fies *et al.* (1987) reported that 25%, 30% and 3% of translocated black bears respectively, repeated nuisance behaviour. Shivik *et al.* (2011) recaptured 4% of black bear involved in nuisance behaviour in Wisconsin that were trapped at agricultural areas and translocated 40 to 64 km. Our observations may underestimate the degree of nuisance behaviour by excluding complaints resolved with technical assistance over the phone (Voyles *et al.* 2015). However, these complaints are generally deemed less serious (e.g. not involving agriculture or property damage) than are those resulting in translocation. In Wisconsin, most of complaints not involving agriculture or property damage were resolved over the phone (D. Ruid, unpubl. data), highlighting the value of public education and outreach in these situations. The small proportion of recaptured translocated bears, therefore, suggests a low repeated incidence of more serious nuisance behaviours, although we lacked the data to explicitly test this hypothesis. Our low recapture rates could also be due to hunter harvest, because 38% of translocated bears were harvested by hunters, and other non-harvest mortalities. However, our overall recapture rates were similar with and without excluding bears that were recovered dead.

In contrast to the low recurrence of nuisance behaviour, 36% of translocated black bears involved in nuisance behaviour that were recaptured occurred outside of what we defined as their original home range. Although this percentage refers only to bears that were recaptured resuming nuisance behaviour, return probability may still be an important measure of translocation success because the objective of many translocations may, indeed, be to remove nuisance individuals from particular areas or properties. However, although translocation may reduce the incidence of nuisance behaviour for particular individuals, it may have less efficacy for reducing nuisance complaints on particular properties by other bears (Voyles *et al.* 2015).

Our results also show how the definition of translocation success can influence subsequent management recommendations. We found a weak association between translocation distance over a range of 2 to 235 km and the probability of repeated nuisance behaviour. In contrast, we observed a strong negative association between return probability and translocation distance over a range of 19 to 124 km for yearling bears. Despite the low probability of repeated nuisance behaviour in our study, we still recommend that managers consider increasing translocation distance when deciding where to translocate black bears in Wisconsin, as this will likely reduce the probability of a bear returning to its original home range. Our higher rates of repeated nuisance behaviour for bears with multiple translocation events may also suggest that some individuals are more prone to repeating nuisance behaviour; however, additional work is needed to test this hypothesis.

Our estimated relationships between translocation distance and age and return probability are consistent with results from previous studies. Multiple studies have reported negative relationships between translocation distance and return probability (Rogers 1986; Linnell *et al.* 1997; Landriault *et al.* 2009). Shivik *et al.* (2011) translocated black bears involved in nuisance

behaviour in Wisconsin agricultural areas 40 to 64 km and found that 15 of 21 recaptures associated with repeated nuisance behaviour occurred  $\leq 10$  km of the bear's capture area. Similar to our study, Landriault *et al.* (2009) found that translocated adult black bears in southern Ontario were far more likely to return than were juveniles (73% vs 29% respectively) and also that the negative effect of translocation distance was stronger for juveniles than for adults. Yearling male black bears are the primary dispersing age class and may disperse  $>200$  km, whereas yearling females generally remain close ( $<15$  km) to their natal home range (Rogers 1987; Costello 2010). However, translocated adult and juvenile bears may still return to their original home range when translocated long distances (100 to 398 km; Rogers 1986; Fies *et al.* 1987; Landriault *et al.* 2006). Adults show a greater degree of home-range fidelity but are also capable of extensive movements outside of their normal home range (Rogers 1987; Costello 2010) and are likely to have greater familiarity with their surrounding landscape because of previous dispersal and extra-home range movements. Higher return rates for adults may, therefore, reflect a greater fitness need for returning to their home range (via familiarity with the location of food resources and potential competitors or mates), increased navigational abilities (Landriault *et al.* 2009), or both.

Our results indicated that the landscape composition around the release site also affects return probability and we observed the strongest effects from agriculture (positive) and forest (negative) land covers. This was reflected in the spatial distribution of return probabilities, wherein probability of return was lowest in the northern, most-forested parts of Wisconsin (Fig. S4). Agricultural landscapes may offer less food, depending on the season (Ditmer *et al.* 2018), shelter, and greater mortality risks, thereby increasing the relative costs of remaining in the release area. Bears may also move more rapidly and extensively in landscapes containing higher proportions of anthropogenically disturbed habitat (Karelus *et al.* 2017; Ditmer *et al.* 2018). Agriculture and forest land covers had the strongest effects at large ( $\geq 75$  km) scales, indicating that the landscape context along the entire return route may affect a bear's ability, willingness to return to its capture area, or both. Alternatively, these broad-scale associations with land cover may reflect regional differences in landscape-scale habitat suitability rather than direct influences of particular land covers. Nevertheless, we recommend that managers not only consider habitat features at potential release sites, but also the broader landscape contexts of the sites.

Most translocated bears in our study were adults, and males were slightly more likely to be recaptured than were females. A similar male-bias has been reported for translocated black bears in Montana (59%, McArthur 1981), Pennsylvania (57%, Alt *et al.* 1977) and the southern Appalachian Mountains (87%, Beeman and Pelton 1976). Landriault *et al.* (2009) found that the sex ratio of captured black bears involved in nuisance behaviour in southern Ontario varied among study sites from equal to 3 : 1 male-biased, indicating that male-bias in black bear nuisance reports is not universal. Male-biased captures of bears involved in nuisance behaviour may be due to more extensive male movement patterns, which may increase their encounters of human food resources or human-dominated landscapes. However, sex had a relatively weak effect on return probability



compared with other covariates, which is consistent with the findings of Landriault *et al.* (2009); however, both our study and theirs found that males were slightly less likely to return than females. This pattern is consistent with the hypothesis that more dispersal-prone individuals (i.e. males) are less likely to return to their release site; however, our limited sample sizes prevented a more rigorous test of this hypothesis.

Our study has shown that translocation can be an effective means of reducing nuisance behaviour and human–wildlife conflict, and has provided guidelines for wildlife managers regarding translocating black bears involved in nuisance behaviour. First, a small minority of translocated bears in our study were recaptured, indicating that translocation across a range of distances (2 to 235 km) strongly reduces nuisance behaviour. Second, translocating yearlings will have the greatest success in removing the individual from the area where nuisance activity occurred. Third, our results also suggest that it may be difficult to prevent adults from returning to their capture location, given their high probability of return across the range of translocation distances employed in our study (i.e.  $\leq 124$  km). Fourth, the landscape context of the release site should be considered across multiple spatial scales, with priority given to release sites in highly forested landscapes. Yet, we encourage additional research to better understand the mechanisms by which landscape context affects post-release movement behaviour of black bears translocated in response to nuisance behaviour. Finally, our results illustrated the management value of providing spatially explicit empirical estimates of translocation success under different scenarios and we recommend the adoption of this approach across studies.

### Conflicts of interest

The authors declare no conflicts of interest.

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