Eat or Be Eaten: Implications of potential exploitative competition between wolves and humans across predator- savvy and -naive deer populations

ELLEN M. CANDLER, *University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA, ORCID: 0000-0002-5810-1942*

STOTRA CHAKRABARTI, *Macalester College, Olin-Rice Science Center 211, St. Paul, MN 55105, USA, ORCID: 0000-0001-8741-4780*

WILLIAM J. SEVERUD, *South Dakota State University, Department of Natural Resource Management, Brookings, South Dakota USA 57006, USA, ORCID: 0000-0003-0150-5986*

JOSEPH K. BUMP, *University of Minnesota, 135 Skok Hall, 2003 Upper Buford Circle, St. Paul, MN 55108, USA, ORCID: 0000-0002-4369-7990*

Abstract

Predator recolonization often evokes innate as well as learnt anti-predatory responses in prey. To test white-tailed deer risk allocation amidst an expanding wolf population in Michigan, we used a paired experimental approach to investigate deer behavior in areas with and without wolves. We treated sites with wolf urine, a novel scent (lemon juice), and a control (distilled water), and used remote cameras to observe deer vigilance, diel activity, and abundance before and after treatment. We also examined the effect of vegetation cover/predator ambush potential on deer vigilance. For most deer-response metrics, wolf urine had no effect irrespective of actual wolf presence or absence. However, we observed a difference in the overall diel pattern of deer in areas with wolf presence versus without. Further, we detected significant shifts in diel activity in both areas pre- and post-treatment. While such shifts were not consistent, we could detect a reduction in crepuscular deer activity in areas where deer coexist with wolves. While deer vigilance was typically unaffected by treatments, habitat cover was found to be pivotal. We observed a significant positive effect of vegetation cover on deer vigilance at sites where wolves were present. These results likely indicate that predator cues affect deer vigilance more acutely in denser habitats, which presumably facilitate higher predator success. We did not observe a similar response in the *predator-naive* deer population. In areas where human and non-human predators hunt the same prey, predator presence may thus negatively impact human hunting success through exploitative competition by making deer more vigilant. However, hunters may avoid such competition by choosing hunting/bait sites located in open areas. Our results on fundamental predation ecology have strong applied implications for fostering human-predator coexistence.

Key words: behavioural manipulation, human-wildlife conflict, olfactory cues, optimal foraging, predator-prey interactions, predator reintroduction

Background

Predators can alter prey populations directly through lethal offtake and/or behaviourally mediated indirect effects [1–3]. While some prey succumb, others avoid predation by changing their behaviour and life-histories [4,5]. Predator-effects on prey are a fundamental focus in ecology, although, dynamic predator-prey interactions in a fast-changing Anthropocene warrant more experimental examinations of the underlying mechanisms of these direct and indirect effects [6,7]. While predator populations are declining in many parts of the world [8], some areas are witnessing their comebacks [9–11]. Such contrasting levels of predator presence create (and re-create) intriguing interactions. Predators recolonizing previously predator-free habitats may encounter potentially naive prey that have lost anti-predatory strategies [12,13].

Anti-predator responses are defence strategies that prey species employ when they perceive predation risk via visual, auditory, tactile, and/or olfactory stimuli. When at risk, prey respond through multiple mechanisms either proactively, such as by increasing vigilance, avoiding risky areas, social grouping, and birth synchrony, or reactively through evasion, camouflage, and defence-herding [5,14–17]. Successful anti-predatory responses, while providing survival benefits, can have severe fitness costs for individuals. For example, ungulates that are known to intensify vigilance as a response to predator cues limit durations of feeding or avoid high-risk areas even if they are rich with resources [2,18–21]. Furthermore, certain herbivores are known to incur major reproductive costs while courting at breeding grounds that also attract a host of predators [22,23]. However, perception and response to predation risk have significant decision-making implications that can result from a mix of instinctive and learnt

behaviours. Thus, the risk of predation can vary greatly amongst experienced prey (prey that live under constant predation pressure) versus naive prey (prey that live without or under low predation pressure). For example, in areas where wolves (*Canis lupus*) and grizzly bears (*Ursus horribilis*) had been extirpated, moose (*Alces alces*) did not exhibit avoidance to predator olfactory or auditory cues, while those that had been exposed to both predators showed avoidance [12]. Similarly, species on predator-free islands have been observed to 'adaptively forget' anti-predatory strategies, resulting in prey naivety [24]

The Upper and Lower Peninsula (UP and LP) of Michigan, USA offers a novel opportunity to explore these drivers of predator-effects. In the LP, white-tailed deer (*Odocoileus virginianus*) occur where wolves have been functionally absent since the mid-1800s; while deer in the nearby UP coexist with a re-established wolf population since the mid-2010s [25]. Also, white-tailed deer are a subsistence species for indigenous populations and a highly valued hunting species in this region. In Michigan, deer are typically hunted by humans at specific locations where deer are acclimatized with bait consisting of corn, fruits, or vegetables – creating artificially provisioned resource rich pockets on the landscape. These resource-rich but localized hunter-bait sites are intended to attract and condition deer to revisit these sites frequently. According to behavioural optimality, prey species need to balance the conflicting demands of efficient foraging and predator avoidance [26,27]. Thus, deer behaviour at these hunter-bait sites is expected to be mediated by the perceived risk of predation because wolves are attracted to bait sites as well [28], which in turn should be influenced by prey experience or naivety towards predators.

Through a paired experimental design, we tested for differences in risk perception by examining the immediate behavioural effects of wolf olfactory cues on naive versus experienced

deer at hunter-bait sites. Whereas we expected no response from naive deer (LP deer; no wolf population) to wolf scent (urine), we predicted deer that generally experience wolf predation (UP) would increase group size, intensity of vigilance, and occur less often at bait sites with wolf cues (scent). We also predicted that the immediate effects of predator cues on deer vigilance will be further modulated by habitat covariates such as vegetation cover at the sites. Prey are often cautious, and tend to avoid 'risky' areas that lack good visibility and offer ambushing opportunities for predators even where food is abundant [2,29,30]. Additionally, in accordance with the predation risk allocation hypothesis that suggests temporal variation in predation risk severity will affect foraging and vigilance behaviour in prey [27], we predicted that experienced deer would adjust their activity patterns to avoid crepuscular times when wolves are most active, while naive deer would not make such adjustments.

Methods

Study Area

We conducted the study in Michigan's UP and LP from September 21, 2018 to November 10, 2018. The UP study area was entirely within the Hiawatha National Forest and was interspersed with unpaved, forest service roads. While the bait sites in the LP study area were all located in Mackinaw State Forest of Michigan, the study area was also interspersed with private agriculture, forestland, and paved, secondary roads (Figure 1). The main vegetation cover, derived from the National Land Cover Database (NLCD), at the UP study sites was evergreen (5 sites), woody wetland (3 sites), grassland (3 sites), deciduous (2 sites), and mixed forest (2 sites), while the LP study sites were deciduous (6 sites), scrub/shrub (4 sites), grassland (3 sites), and evergreen (2 sites; Figure 1) [31].

Study Design

115 We established 30 deer bait sites between the two study areas, 15 in the UP and 15 in the LP
116 (Figure 1). To mimic recreational hunters, we selected sites based on deer hunting desirability
117 such as habitat openness and/or proximity to a deer trail [32]. Sites were at least one km away
118 from each other to avoid duplication and dependence [33].

119 We baited each site with 3.8 litres of corn spread in a 3 by 3-meter- square plot, as per the
120 Michigan deer baiting regulations [34]. For the duration of the study, all sites were baited each
121 week in order to maintain 3.8 litres of corn on the ground to replicate actual hunter behaviour
122 and to reduce the confounding effect of bait availability on deer behaviour. We deployed one
123 remote camera (Reconyx Hyperfire series or Cuddeback E) on a tree 4 meters from the centre of
124 the bait site. Each camera was programmed to take 5 burst images with no delay between
125 triggers to record the number of deer present, their posture, sex (when possible), and
126 presence/absence of fawn(s). We replaced batteries and memory cards weekly.

127 We used a 10 week before-after-control-impact (BACI) design for the experimental
128 treatment of both areas with one week preceding the six-week period to establish a baseline
129 condition of deer visitation to the bait sites [35]. For the first three weeks (September 28-October
130 20), we baited sites, recorded deer occurrence and behaviour via remote cameras with no scent
131 treatments applied. For the following three weeks we continued to bait and record deer after
132 treating sites with three scents. In each area, UP and LP, 5 sites were treated each with wolf urine
133 (predator treatment), lemon juice (novel scent; not a native plant), or distilled water (control).
134 We assigned site treatment randomly [20,36]. When we treated sites in the field, we visited all
135 'control' sites in an area first followed by the 'novel scent' sites, and finally 'experimental/wolf
136 urine' sites to avoid cross-site spread of scents. We also used different treatment application
137 tools (i.e. pipets, travel containers) for each treatment type to avoid cross contamination of

138 treatments. At each site, we applied 10 mL of the given treatment (experimental, novel, or
139 control) by dripping it from a pipet onto the bait site. This was done to mimic the amount and
140 application of scent marking of a pair of wolves [37].

141 We also recorded predator concealment or hiding potential (horizontal cover) at each site
142 to account for site-specific differences in habitat openness - an index of perceived predation
143 threat. We used a 2 m cover pole with 20 sections, each 10 cm long, to measure predator hiding
144 potential at each site [38,39]. From the centre of each bait pile, we measured the horizontal cover
145 in each cardinal direction. While one person held the cover pole 10-meters away from the centre
146 of the bait pile, another took a picture of the cover pole with a camera stationed on a 1-meter
147 high pole at the centre of the bait pile, intended to mimic deer visual height [39]. We conducted
148 this procedure twice during the study, once at the beginning and once when treatment started, to
149 account for change in hiding potential with loss of leaves later in the year. For each of the 20 (10
150 cm) sections on the 2 m cover pole, we estimated obscurement to the nearest 25% [39]. We
151 calculated a single mean and standard error value for each site and each measurement time
152 (beginning and middle of study).

153 **Analysis**

154 *Photo Analysis*

155 Images were tagged in batches using the DigiKam photo editing software [40]. Each
156 batch was defined by any set of images taken within 5 minutes of the prior image. In each batch,
157 for deer only, we recorded if fawns were present, labelled all sexes when possible, and tallied a
158 total count. For individual pictures within batches, in addition to generic behaviours (e.g.,
159 fighting, nursing, foraging), we recorded the number of individuals with their heads above their
160 shoulders, indicating vigilance/state of alertness (Figure 2) [14,41]. We also labelled batches for

different species that were captured at site visits including squirrels (*Sciurus* spp.), raccoons (*Procyon lotor*), turkeys (*Meleagris gallopavo*), and coyotes (*Canis latrans*). We did not detect additional scent marking by other species.

Treatment Impact

We explored the impact of different treatments in the two areas (UP and LP) on the number of deer at each site, proportion of group that was vigilant, and the number of visits made to the site. To account for the paired nature of our treatment design, we first averaged the variable values for each site individually and calculated a difference in values before and during treatment application. We then averaged across all sites within a given treatment. We also calculated a vigilance intensity metric using equation 1. This metric includes both group vigilance and event duration.

$$I = \frac{\sum \frac{v}{g}}{e} \qquad \text{(Eq 1)}$$

Where I is the vigilance intensity metric for a given event, v is the number of deer vigilant in a single image, g is the group size in a single image, and e is the total time of the event. Hence, vigilance intensity simply standardizes individual vigilance across different group sizes and time spent in front of the camera. Similar to the previous analysis, we calculated a difference in vigilance intensity before and after treatment for each treatment type in each peninsula.

Diel Activity

To analyse possible temporal variability in the use of bait sites in the UP and LP before and after treatment, we used a nonparametric kernel density estimation procedure [42,43]. We converted times to radians and used a kernel density estimator to create a probability density distribution for each before or after period [44]. We calculated the proportion of temporal

overlap between the two treatment periods for each treatment in an area [42]. We used a $\hat{\Delta}_4$ with a smoothing parameter of 1 because our sample size for all analyses was greater than 50 [44]. We conducted this analysis using the overlap package [42,45] in R.

We applied Watson's U2 statistic with the CircStats package to test for homogeneity between the two samples of interest (i.e. test for/detect a statistically significant shift in the diel pattern before and after treatment) [46,47]. If deer significantly shifted their temporal pattern between the two treatment periods, we expected Watson's U2 statistic would be greater than the critical value (0.19 for an α value of 0.05) and $P < 0.05$. In the UP, we predicted that there would be no shift in temporal visitation by deer at the control and lemon treated sites (high $\hat{\Delta}_4$, $U2 \leq 0.19$), while a shift to more nocturnal activity at the wolf urine treated sites would be detected (lower $\hat{\Delta}_4$, $U2 > 0.19$; Kohl et al. 2018) to potentially avoid wolves that are known to be typically less active at night [5]. In the LP, we expected that we would not see a significant shift in any treatment sites because deer in the LP are ostensibly naive to wolf predation.

Vegetation Cover Analysis

We fitted generalized linear models using pooled data from both the UP and LP to check for the effect on overall vigilance intensity by treatment effect (before/after) and type (predator/novel/control), area (UP or LP) and vegetation cover (i.e., predator hiding potential; S1) [43,48] through additive and interactive effects between parameters of interest. Subsequently, we fitted models to examine the relationship between vigilance intensity and vegetation cover at each treatment type within both the UP and LP before and after treatment.

Results

We obtained 286,436 images over seven weeks. After removing images taken during the pre-experimental, baseline week and images that did not contain deer, we had 213,264 images for analysis with 85,675 images taken in the LP and 127,589 images taken in the UP.

We observed a near 30% increase in group size at sites treated with wolf urine in the UP but this increase translates to less than half a deer, an increase that is not ecologically meaningful. Additionally, we observed a slight increase (<0.03) in the number of visits at both lemon and control treated sites in the UP and a marginal decrease (<0.04) in the proportion of the group that was vigilant at lemon treated sites in the LP (Table 1, Figure 3). We also observed a decrease in vigilance intensity of deer at wolf urine treated sites in the LP (Figure 3). We did not detect a significant change before and after treatments for any other treatment sites in either area for the four response variables, i.e., the proportion of group that is vigilant, number of visits, and vigilance intensity (Figure 3).

Table 1. Perceived effect of wolf (*Canis lupus*) predation risk on deer behaviour. Mean difference before treatment period and during treatment period in group vigilance, group size, number of visits, and vigilance intensity (sum of proportion of group vigilance in each event divided by total time of event) from September to November 2018 in the Upper Peninsula (UP) and Lower Peninsula (LP) Michigan, USA. *Differences before treatment period and during treatment periods were significant if the 95% confidence interval did not include 0.

Area	Response variable	Treatment	Mean difference	95% CI
UP	Group vigilance	wolf	-0.044	-0.101 to 0.013
		lemon	-0.032	-0.082 to 0.017
		control	-0.020	-0.071 to 0.031
	Group size	wolf	0.293*	0.093 to 0.492
		lemon	0.238	-0.159 to 0.635
		control	0.166	-0.018 to 0.351

	Number of visits	wolf	0.011	-0.020 to 0.043
		lemon	0.024*	0.011 to 0.037
		control	0.007*	0.003 to 0.011
	Vigilance intensity	wolf	0.001	-0.021 to 0.024
		lemon	-0.008	-0.024 to 0.007
		control	-0.010	-0.023 to 0.003
LP	Group vigilance	wolf	-0.007	-0.083 to 0.068
		lemon	-0.035*	-0.044 to -0.025
		control	0.016*	0.002 to 0.034
	Group size	wolf	-0.341	-1.294 to 0.611
		lemon	0.133	-0.061 to 0.327
		control	-0.110	-0.626 to 0.405
	Number of visits	wolf	0.004	-0.019 to 0.012
		lemon	0.001	0.002 to 0.004
		control	0.000	-0.065 to 0.065
	Vigilance intensity	wolf	-0.028	-0.055 to 0.001
		lemon	0.002	-0.012 to 0.008
		control	0.008	-0.010 to 0.026

Deer changed their diel activity in the LP and UP, and in all treatment types, before and after treatment application (i.e., all U2 > 0.19). We did not detect a consistent directional pattern in the temporal shifts for most sites. However, we did observe a difference between the UP and LP diel patterns where the deer in the UP tended to reduce activity between 6:00 and 18:00 both before and after treatment application while the deer in the LP did not have a consistent inactivity period (Figure 4). Additionally, deer at wolf-treated sites in the UP reduced bait site visitation in the evening hours (i.e., 1800h; Figure 4).

Deer vigilance intensity increased by 1.3 times for unit increase in vegetation cover in the UP but not in the LP (Figure 5; S1). Though vigilance intensity did not increase with vegetation cover in the LP, the base vigilance intensity (model intercepts) increased significantly after all treatment applications (S2).

240 **Discussion**

241 Predator absence for long durations can lead to the gradual erosion of anti-predatory
242 responses of prey [12,13]. Subsequent recolonization of predators to such landscapes raises
243 questions about the response that naive prey will have once predators return, particularly in prey
244 populations valued and pursued by human hunters. We investigated the effects of simulated
245 predator presence on experienced versus naive deer at food-rich hunter-bait sites. We did not
246 find a significant effect of wolf scent treatment on deer vigilance, number of visits, or vigilance
247 intensity among predator-savvy/experienced deer in the UP but did note a slight increase in
248 group size, though the difference was not ecologically meaningful. A lack of response to wolf
249 urine has been documented in deer populations in the Netherlands and Poland where little
250 support was found for effects of predator scents in both predator savvy and predator naive prey
251 populations even when three times the volume of wolf urine was used [49]. This lack of reaction
252 to wolf scent cues in both areas may also be a result of decreasing response over time to the wolf
253 urine as it degrades [2,20,50]. Introducing cues that indicate immediate wolf proximity, such as
254 howling or visual, are likely to produce different results [49,51]. The absence of any response to
255 wolf urine may also be a result of predator hunting strategies. Cursorial predators might fail to
256 evoke strong anti-predatory responses in deer, as opposed to pronounced effects as observed in
257 the case of cues from ambush predators [52,53].

258 We also observed a significant shift in diel patterns at all sites before and after treatment
259 but there was no consistency to the shift in activity for most treatment sites. However, deer at
260 sites treated with wolf scent in the UP (where they coexist with wolves) reduced their visitation
261 in the evening hours. This finding is in accordance with other research that suggests that ungulate
262 prey shift their activity to avoid riskier times [5,54]. For example, deer in Minnesota, USA

263 demonstrated a more diurnal pattern under the effects of wolf scent to likely avoid the riskier
264 crepuscular times when wolves tend to hunt [1]. It is also noteworthy that before and after
265 treatment application, all UP sites exhibited a decrease in deer activity at bait sites between 6:00
266 and 18:00 hours, while the LP sites had inconsistent patterns. This suggests that deer in the UP
267 are perhaps avoiding peak wolf activity/hunting hours regardless of cues at sites, while LP deer
268 do not have as large of an inactivity period, likely because they do not share habitat with wolves
269 (S2; [5]).

270 Our results show a strong correlation of vigilance intensity with vegetation cover where
271 wolves are established. Increase in vegetation cover at the UP sites were characterized by intense
272 vigilance activity in deer, regardless of treatment. Thicker vegetation likely represents more
273 predator hiding potential and difficult escape routes, likely causing an increase in deer vigilance
274 regardless of olfactory cues at the site (Figure 5) [20,55,56]. Research comparing white-tailed
275 deer and mule deer (*Odocoileus hemionus*) in Oregon's expanding wolf range reported that
276 white-tailed deer did not typically avoid areas with wolves but did favour areas with less dense
277 vegetation that facilitates an easy escape because they relied on flight and early detection of
278 predators [55]. Alternatively, mule deer avoided areas where wolves were present altogether
279 because they relied on a stotting gait that is advantageous in uneven areas with more obstacles.
280 This phenomenon has also been noted in other species such as chacma baboons (*Papio ursinus*)
281 in Gorongosa National Park, Mozambique where vocalization and vigilance were heightened in
282 denser habitats [57]. Our findings further highlight the importance of considering prey behaviour
283 and escape strategies, along with habitat characteristics for a mechanistic understanding of
284 predator-effects.

285 Though vegetation cover did not have a significant effect at LP sites, deer at wolf urine
286 treated sites did demonstrate higher baseline vigilance intensity after treatment was applied but it
287 did not vary across vegetation cover. This suggests that naive deer may demonstrate an innate
288 fear of wolves, also reported in East Limestone Island, Canada [19]. However, when the novel
289 scent (lemon) and control sites were assessed in the same context, we saw a similar pattern
290 indicating that something other than predator scent might be affecting baseline vigilance later in
291 the study. Since the second half of the study was conducted during archery hunting season, this
292 shift in vigilance may indicate a response to increased human presence [58]. Research in Poland
293 found that red deer (*Cervus elaphus*) demonstrated heightened vigilance during hunting season
294 when hunters were likely pursuing them [59].
295 Our findings give partial support to the predator risk allocation hypothesis by showing a
296 shift in activity by prey with predator experience to a less risky feeding time for prey that
297 experience a pause in predation pressure when predators are less active [5,27]. This hypothesis
298 may also explain the lack of difference in vigilance detected in the UP-deer population in
299 relation to the wolf urine treatment. Because this population is under constant predation pressure
300 from wolves and frequently encounters wolf cues, deer in the UP may demonstrate a change of
301 vigilance especially at food rich site such as hunter-bait sites, in order to take advantage of the
302 food source as quickly as possible. Deer in the UP are also likely, as we observed, to show more
303 vigilance intensity in areas with higher predation potential, such as high vegetation cover [55].
304 Finally, through our experimental study we highlight the importance of considering both
305 spatial and temporal factors when understanding predator effects on experienced versus naive
306 prey. Past research has suggested that naive prey do not maintain the innate ability to react to
307 predator olfactory cues but do have the ability to learn and adjust to predators within one

generation [12,60]. Though olfactory cues did not have a significant effect on most variables we investigated, we did observe a strong predator effect depending on vegetation cover that ostensibly modifies risk.

The recreational hunting tradition of baiting is controversial inside and outside the hunting community. Baiting increases the opportunity for a successful shot and more immediate kill, but also creates a predictable food source that concentrates deer and deer scent, which in turn attracts wolves [61]. As large predators continue to recolonize their former ranges, they will inevitably overlap with human hunters [62,63]. Our current research can shed light on the impact a predator has on a predator savvy and predator naive prey population as it relates to hunting by humans. We show that predator cues can affect deer vigilance at bait-sites with thicker vegetation, seemingly making deer wary and difficult to hunt, thereby potentially affecting the experience and satisfaction reported in hunter surveys. However, we urge readers, managers, and the hunting community to interpret our results cautiously and constructively. Our results can be formative in aiding carnivore-human coexistence wherein human hunters can have more success if they potentially choose not to bait/hunt deer at vegetatively dense sites.

Acknowledgements

This material is based upon work supported by the National Science Foundation Graduate Research Fellowship Program under Grant No. 00039218. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation. This research was also supported by grants from the National Science Foundation to J. K. Bump (NSF ID#1545611, NSF ID#1556676). We thank M. Dean, K. Rajski, and A. Schubel for field assistance.

Author Contributions

E.M.C.: idea formulation, sampling design, data collection, formal analysis, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; S.C.: sampling design, methodology, validation, visualization, writing—review and editing; W.J.S.: sampling design, methodology, writing—review and editing, J.K.B.: idea formulation, sampling design, project administration, writing—review and editing, funding acquisition, supervision, resources

Literature Cited

1. Palmer MS, Portales-Reyes C, Potter C, Mech LD, Isbell F. 2021 Behaviorally-mediated trophic cascade attenuated by prey use of risky places at safe times. *Oecologia* **195**, 235–248. (doi:10.1007/s00442-020-04816-4)

2. Kuijper DPJ, de Kleine C., Churski M., van Hooft P., Bubnicki J., Jędrzejewska B. 2013 Landscape of fear in Europe: Wolves affect spatial patterns of ungulate browsing in Białowieża Primeval Forest, Poland. *Ecography* **36**, 1263–1275. (doi:10.1111/j.1600-0587.2013.00266.x)

3. McNay RS, Lamb CT, Giguere L, Williams SH, Martin H, Sutherland GD, Hebblewhite M. 2022 Demographic responses of nearly extirpated endangered mountain caribou to recovery actions in Central British Columbia. *Ecological Applications* **n/a**, e2580. (doi:10.1002/eap.2580)

4. Sabal MC *et al.* 2021 Predation landscapes influence migratory prey ecology and evolution. *Trends in Ecology & Evolution* **36**, 737–749. (doi:10.1016/j.tree.2021.04.010)

5. Kohl MT, Stahler DR, Metz MC, Forester JD, Kauffman MJ, Varley N, White PJ, Smith DW, MacNulty DR. 2018 Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* **0**, 1–15. (doi:10.1002/ecm.1313)

6. Scrosati RA. 2021 Nonconsumptive predator effects on prey demography: Recent advances using intertidal invertebrates. *Frontiers in Ecology and Evolution* **9**.

7. Parsons MA, Newsome TM, Young JK. 2022 The consequences of predators without prey. *Frontiers in Ecology and the Environment* **20**, 31–39. (doi:10.1002/fee.2419)

8. Ripple WJ *et al.* 2014 Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484. (doi:10.1126/science.1241484)

9. Scharf AK, Fernández N. 2018 Up-scaling local-habitat models for large-scale conservation: Assessing suitable areas for the brown bear comeback in Europe. *Diversity and Distributions* **24**, 1573–1582. (doi:10.1111/ddi.12796)

10. Jarausch A, Harms V, Kluth G, Reinhardt I, Nowak C. 2021 How the west was won: genetic reconstruction of rapid wolf recolonization into Germany's anthropogenic landscapes. *Heredity* **127**, 92–106. (doi:10.1038/s41437-021-00429-6)

11. Gigliotti LC, Matchett MR, Jachowski DS. 2019 Mountain lions on the prairie: Habitat selection by recolonizing mountain lions at the edge of their range. *Restoration Ecology* **27**, 1032–1040. (doi:10.1111/rec.12952)

12. Berger J, Swenson JE, Persson I-L. 2001 Recolonizing carnivores and naïve prey: Conservation lessons from pleistocene extinctions. *Science* **291**, 1036–1039. (doi:10.1126/science.1056466)

13. Berger J. 1999 Anthropogenic extinction of top carnivores and interspecific animal behaviour: Implications of the rapid decoupling of a web involving wolves, bears, moose and ravens. *Proc. R. Soc. Lond. B* **266**, 2261–2267. (doi:10.1098/rspb.1999.0917)

14. Flagel DG, Belovsky GE, Beyer DE. 2016 Natural and experimental tests of trophic cascades: Gray wolves and white-tailed deer in a Great Lakes forest. *Oecologia* **180**, 1183–1194. (doi:10.1007/s00442-015-3515-z)

15. Ims RA. 1990 On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The American Naturalist* **136**, 485–498. (doi:10.1086/285109)

16. Rowland HM, Burriss RP, Skelhorn J. 2020 The antipredator benefits of postural camouflage in peppered moth caterpillars. *Sci Rep* **10**, 21654. (doi:10.1038/s41598-020-78686-4)

17. Mech LD. 2007 Possible use of foresight, understanding, and planning by wolves hunting muskoxen. *Arctic* **60**, 145–149.

18. Melchiors MA, Leslie CA. 1985 Effectiveness of Predator Fecal Odors as Black-Tailed Deer Repellents. *The Journal of Wildlife Management* **49**, 358–362. (doi:10.2307/3801531)

19. Chamaillé-Jammes S, Malcuit H, Saout SL, Martin J-L. 2014 Innate threat-sensitive foraging: Black-tailed deer remain more fearful of wolf than of the less dangerous black bear even after 100 years of wolf absence. *Oecologia* **174**, 1151–1158. (doi:10.1007/s00442-013-2843-0)

20. Wikenros C, Kuijper DPJ, Behnke R, Schmidt K. 2015 Behavioural responses of ungulates to indirect cues of an ambush predator. *Behaviour* **152**, 1019–1040. (doi:10.1163/1568539X-00003266)

21. Sahlén E, Noell S, DePerno CS, Kindberg J, Spong G, Cromsigt JPGM. 2016 Phantoms of the forest: Legacy risk effects of a regionally extinct large carnivore. *Ecol Evol* **6**, 791–799. (doi:10.1002/ece3.1866)

22. Jhala YV, Isvaran K. 2016 Behavioural ecology of a grassland antelope, the blackbuck antilope cervicapra: Linking habitat, ecology and behaviour. In *The Ecology of Large Herbivores in South and Southeast Asia* (eds FS Ahrestani, M Sankaran), pp. 151–176. Dordrecht: Springer Netherlands. (doi:10.1007/978-94-017-7570-0_6)

23. Cherry MJ, Morgan KE, Rutledge BT, Conner LM, Warren RJ. 2016 Can coyote predation risk induce reproduction suppression in white-tailed deer? *Ecosphere* **7**, e01481. (doi:10.1002/ecs2.1481)

24. Blumstein DT, Daniel JC, Springett BP. 2004 A test of the multi-predator hypothesis: Rapid loss of antipredator behavior after 130 years of isolation. *Ethology* **110**, 919–934. (doi:10.1111/j.1439-0310.2004.01033.x)

25. O'Neil ST, Bump JK, Beyer DE. 2017 Spatially varying density dependence drives a shifting mosaic of survival in a recovering apex predator (*Canis lupus*). *Ecology and Evolution* **7**, 9518–9530. (doi:10.1002/ece3.3463)

26. Sih A. 1980 Optimal behavior: Can foragers balance two conflicting demands? *Science* **210**, 1041–1043. (doi:10.1126/science.210.4473.1041)

27. Lima SL, Bednekoff PA. 1999 Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *The American Naturalist* **153**, 649–659. (doi:10.1086/303202)

28. Bump JK, Murawski CM, Kartano LM, Beyer DEJr, Roell BJ. 2013 Bear-baiting may exacerbate wolf-hunting dog conflict. *PLOS ONE* **8**, e61708. (doi:10.1371/journal.pone.0061708)

29. Edwards J. 1983 Diet shifts in moose due to predator avoidance. *Oecologia* **60**, 185–189. (doi:10.1007/BF00379520)

30. Ripple WJ, Beschta RL. 2004 Wolves and the ecology of fear: Can predation risk structure ecosystems? *BioScience* **54**, 755–766. (doi:10.1641/0006-3568(2004)054[0755:WATEOF]2.0.CO;2)

31. Homer C, Dewitz J, Yang L, Jin S, Danielson P, Coulston J, Herold N, Wickham J, Megown K. 2015 Completion of the 2011 national land cover database for the conterminous United States – representing a decade of land cover change information. *PHOTOGRAMMETRIC ENGINEERING* , 11.

32. Peterson TJ. 2015 5 best funnel & pinch-point setups for hunting whitetails. *Game & Fish*. See https://www.gameandfishmag.com/editorial/5-best-funnel-pinch-point-setups-for-hunting-whitetails/191246.

33. Winke B. 2012 Can deer tell how far away a source of an odor Is? *Petersen's Bowhunting*. See https://www.bowhuntingmag.com/editorial/can-deer-tell-how-far-away-a-source-of-an-odor-is/309382.

34. Michigan Department of Natural Resources. 2018 Michigan Hunting Digest.

35. Stewart-Oaten A, Murdoch WW, Parker KR. 1986 Environmental impact assessment: 'Pseudoreplication' in time? *Ecology* **67**, 929–940. (doi:10.2307/1939815)

36. Atkins R, Blumstein DT, Moseby KE, West R, Hyatt M, Letnic M. 2016 Deep evolutionary experience explains mammalian responses to predators. *Behav Ecol Sociobiol* **70**, 1755–1763. (doi:10.1007/s00265-016-2181-4)

37. Peters RP, Mech LD. 1975 Scent-Marking in wolves: Radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well. *American Scientist* **63**, 628–637.

38. Kuijper DPJ, Verwijmeren M, Churski M, Zbyryt A, Schmidt K, Jędrzejewska B, Smit C. 2014 What cues do ungulates use to assess predation risk in dense temperate forests? *PLOS ONE* **9**, e84607. (doi:10.1371/journal.pone.0084607)

39. Severud WJ, DelGiudice GD, Obermoller TR. 2019 Association of moose parturition and post-parturition habitat with calf survival. *The Journal of Wildlife Management* **83**, 175–183. (doi:https://doi.org/10.1002/jwmg.21570)

40. Niedballa J, Sollmann R, Courtiol A, Wilting A. 2016 camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution* **7**, 1457–1462. (doi:https://doi.org/10.1111/2041-210X.12600)

41. Schuttler SG, Parsons AW, Forrester TD, Baker MC, McShea WJ, Costello R, Kays R. 2017 Deer on the lookout: How hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of Zoology* **301**, 320–327. (doi:https://doi.org/10.1111/jzo.12416)

42. Wang Y, Allen ML, Wilmers CC. 2015 Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation* **190**, 23–33. (doi:10.1016/j.biocon.2015.05.007)

43. Prugh LR, Sivy KJ, Mahoney PJ, Ganz TR, Ditmer MA, van de Kerk M, Gilbert SL, Montgomery RA. 2019 Designing studies of predation risk for improved inference in carnivore-ungulate systems. *Biological Conservation* **232**, 194–207. (doi:10.1016/j.biocon.2019.02.011)

44. Ridout MS, Linkie M. 2009 Estimating overlap of daily activity patterns from camera trap data. *JABES* **14**, 322–337. (doi:10.1198/jabes.2009.08038)

45. Meredith M, Ridout M. 2018 overlap: Estimates of coefficient of overlapping for animal activity patterns.

46. Lund U, Agostinelli C. 2012 CircStats: Circular statistics, from 'topics in circular statistics' (2001).

47. Lashley MA, Cove MV, Chitwood MC, Penido G, Gardner B, DePerno CS, Moorman CE. 2018 Estimating wildlife activity curves: Comparison of methods and sample size. *Scientific Reports* **8**, 1–11. (doi:10.1038/s41598-018-22638-6)

48. Fležar U, le Roux E, Kerley GIH, Kuijper DPJ, te Beest M, Druce DJ, Prinsloo D, Cromsigt JPGM. 2019 Simulated elephant-induced habitat changes can create dynamic landscapes of fear. *Biological Conservation* **237**, 267–279. (doi:10.1016/j.biocon.2019.07.012)

49. van Ginkel HAL, Smit C, Kuijper DPJ. 2019 Behavioral response of naïve and non-naïve deer to wolf urine. *PLOS ONE* **14**, e0223248. (doi:10.1371/journal.pone.0223248)

50. Bytheway JP, Carthey AJR, Banks PB. 2013 Risk vs. reward: How predators and prey respond to aging olfactory cues. *Behav Ecol Sociobiol* **67**, 715–725. (doi:10.1007/s00265-013-1494-9)

51. Liley S, Creel S. 2008 What best explains vigilance in elk: Characteristics of prey, predators, or the environment? *Behavioral Ecology* **19**, 245–254. (doi:10.1093/beheco/arm116)

52. Preisser EL, Orrock JL, Schmitz OJ. 2007 Predator Hunting Mode and Habitat Domain Alter Nonconsumptive Effects in Predator–Prey Interactions. *Ecology* **88**, 2744–2751. (doi:10.1890/07-0260.1)

53. Sunde P, Böcker F, Rauset GR, Kjellander P, Chrenkova M, Skovdal TM, van Beeck Calkoen S, Mayer M, Heurich M. 2022 Mammal responses to predator scents across multiple study areas. *Ecosphere* **13**, e4215. (doi:10.1002/ecs2.4215)

54. Gehr B, Hofer EJ, Ryser A, Vimercati E, Vogt K, Keller LF. 2018 Evidence for nonconsumptive effects from a large predator in an ungulate prey? *Behav Ecol* **29**, 724–735. (doi:10.1093/beheco/ary031)

55. Dellinger JA, Shores CR, Craig A, Heithaus MR, Ripple WJ, Wirsing AJ. 2019 Habitat use of sympatric prey suggests divergent anti-predator responses to recolonizing gray wolves. *Oecologia* **189**, 487–500. (doi:10.1007/s00442-018-4323-z)

56. van Ginkel HAL, Kuijper DPJ, Schotanus J, Smit C. 2019 Wolves and tree logs: Landscape-scale and fine-scale risk factors interactively influence tree regeneration. *Ecosystems* **22**, 202–212. (doi:10.1007/s10021-018-0263-z)

57. Hammond P, Lewis-Bevan L, Biro D, Carvalho S. In press. Risk perception and terrestriality in primates: A quasi-experiment through habituation of chacma baboons (Papio ursinus) in Gorongosa National Park, Mozambique. *American Journal of Biological Anthropology* **n/a**. (doi:10.1002/ajpa.24567)

58. Benhaiem S, Delon M, Lourtet B, Cargnelutti B, Aulagnier S, Hewison AJM, Morellet N, Verheyden H. 2008 Hunting increases vigilance levels in roe deer and modifies feeding site selection. *Animal Behaviour* **76**, 611–618. (doi:10.1016/j.anbehav.2008.03.012)

59. Proudman NJ *et al.* 2020 Red deer allocate vigilance differently in response to spatio-temporal patterns of risk from human hunters and wolves. *Wildl. Res.* **48**, 163–174. (doi:10.1071/WR20059)

60. Steindler LA, Blumstein DT, West R, Moseby KE, Letnic M. 2020 Exposure to a novel predator induces visual predator recognition by naïve prey. *Behav Ecol Sociobiol* **74**, 102. (doi:10.1007/s00265-020-02884-3)

61. Hughes NK, Price CJ, Banks PB. 2010 Predators are attracted to the olfactory signals of prey. *PLOS ONE* **5**, e13114. (doi:10.1371/journal.pone.0013114)

62. Bled F *et al.* 2022 Balancing carnivore conservation and sustainable hunting of a key prey species: A case study on the Florida panther and white-tailed deer. *Journal of Applied Ecology* **n/a**. (doi:10.1111/1365-2664.14201)

63. Grima N, Brainard J, Fisher B. 2021 Are wolves welcome? Hunters' attitudes towards wolves in Vermont, USA. *Oryx* **55**, 262–267. (doi:10.1017/S0030605319000061)

532 **Figure Captions**

533 **Figure 1.** Locations of 30 experimental deer bait sites with camera traps deployed between
534 September and November 2018 in Michigan, USA. The top inset map (solid magenta line)
535 indicates the 15 sites in the Upper Peninsula (UP; wolves [*Canis lupus*] present) and the lower
536 inset map (black dashed line) indicates the 15 sites in the Lower Peninsula (LP; wolves absent).
537 The different symbols indicate the different treatments (wolf urine, lemon juice and distilled
538 water) assigned to each site.

539

540 **Figure 2.** Camera-trap detections of white-tailed deer (*Odocoileus virginianus*) at simulated deer
541 hunter-bait sites September to November 2018 in Michigan, USA. The representative images
542 indicate vigilance (A) and non-vigilance (B) behaviour.

543

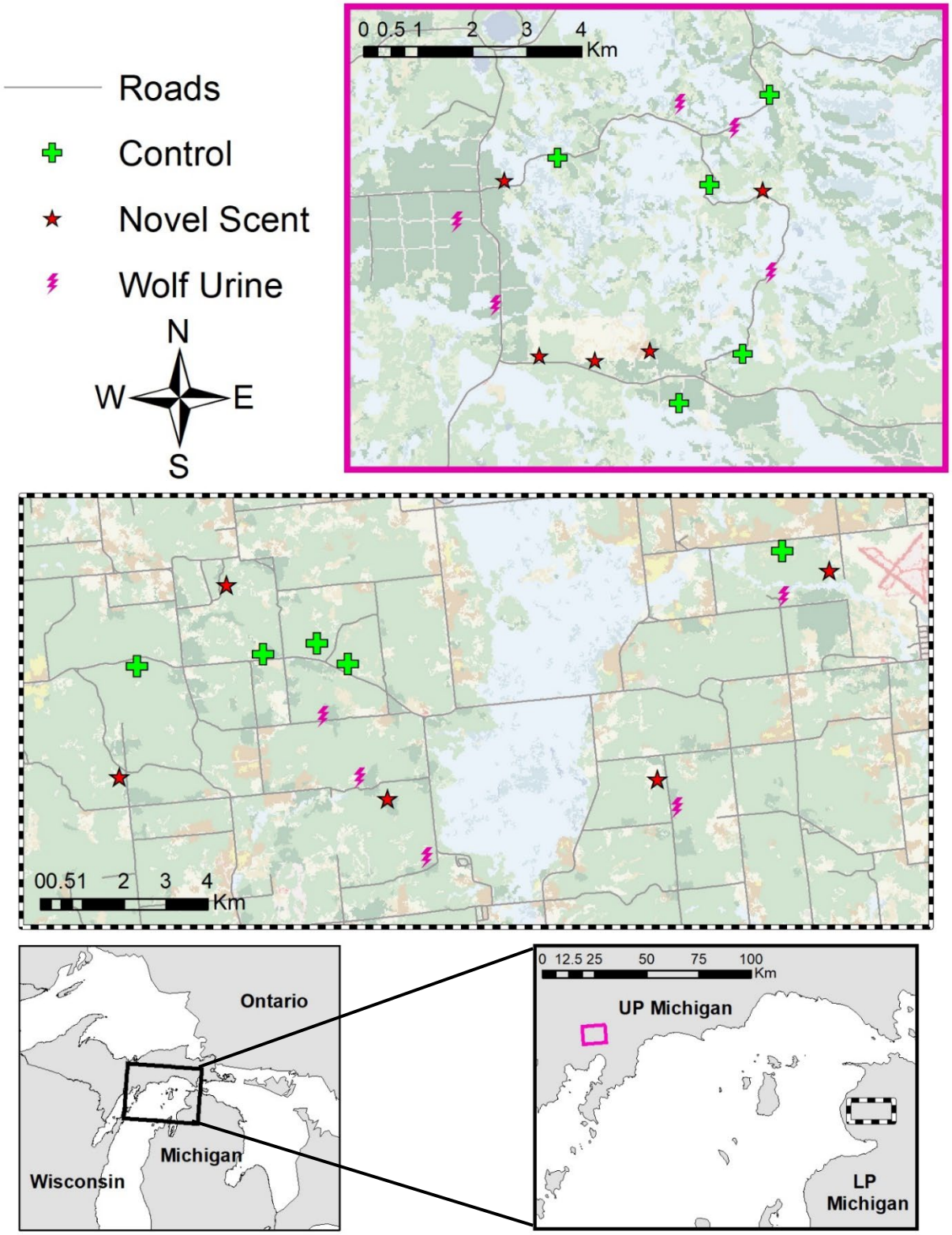
544 **Figure 3.** Perceived effect of wolf (*Canis lupus*) predation risk on deer behaviour. Difference
545 before treatment period and during treatment period in group size, group vigilance, number of
546 visits, and vigilance intensity (sum of proportion of group vigilance in each event divided by
547 total time of event) from September to November 2018 in Michigan, USA. Symbols indicate the
548 mean difference and error bars indicate 95% confidence interval. Blue shading represents the
549 control sites (water), yellow indicates sites treated with novel scent (lemon), and grey indicates
550 wolf-urine treated sites. Positive values indicate an increase in the metric. Asterix indicates $p <$
551 0.05.

552

553 **Figure 4.** Temporal activity patterns of white-tailed deer (*Odocoileus virginianus*) populations
554 before (solid line) and during treatment application (dashed line) in the Upper Peninsula (UP)

and Lower Peninsula (LP) of Michigan, USA between September and November 2018. Shaded area indicates the temporal overlap between the 2 periods. The orange circle highlights the decrease in deer activity at wolf (*Canis lupus*) urine treated sites in the UP. The reported U2 statistic is evaluated against the test statistic U2 = 0.19.

Figure 5. Effects graph showing the predicted vigilance intensity (sum of proportion of group vigilant in each event divided by total time of event) of white-tailed deer (*Odocoileus virginianus*) by percent vegetation cover for all treatment sites across the Upper Peninsula (UP) of Michigan, USA (A; wolves present); and all treatment sites across the Lower Peninsula (LP) of Michigan, USA (B; wolves [*Canis lupus*] absent).



566

567 Figure 1

Figure 2

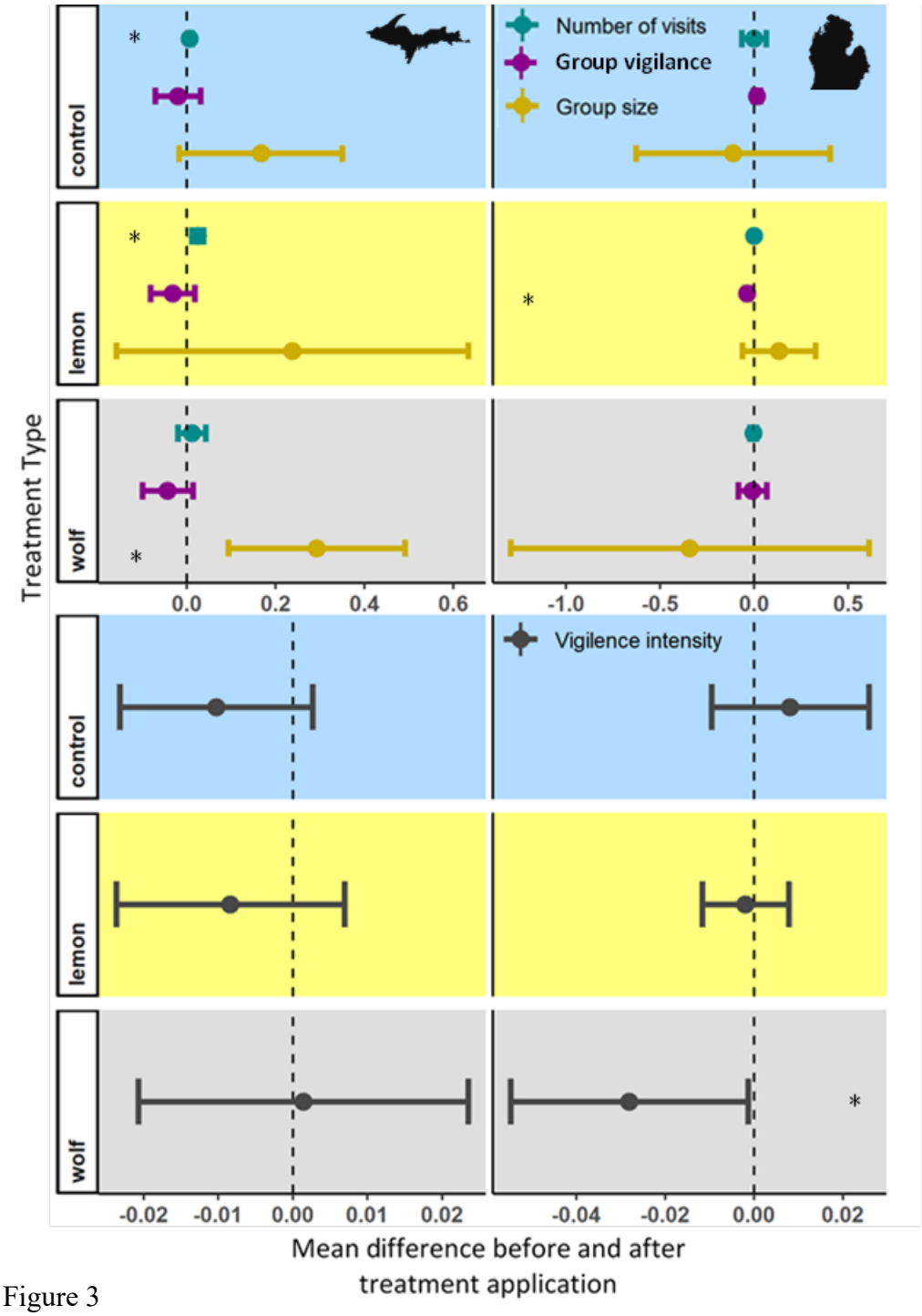

Number of visits
Group vigilance
Group size
Vigilence intensity
Treatment Type
control
lemon
wolf
0.0
0.2
0.4
0.6
-1.0
-0.5
0.0
0.5
-0.02
-0.01
0.00
0.01
0.02
-0.04
-0.02
0.00
0.02
Mean difference before and after treatment application

Figure 3

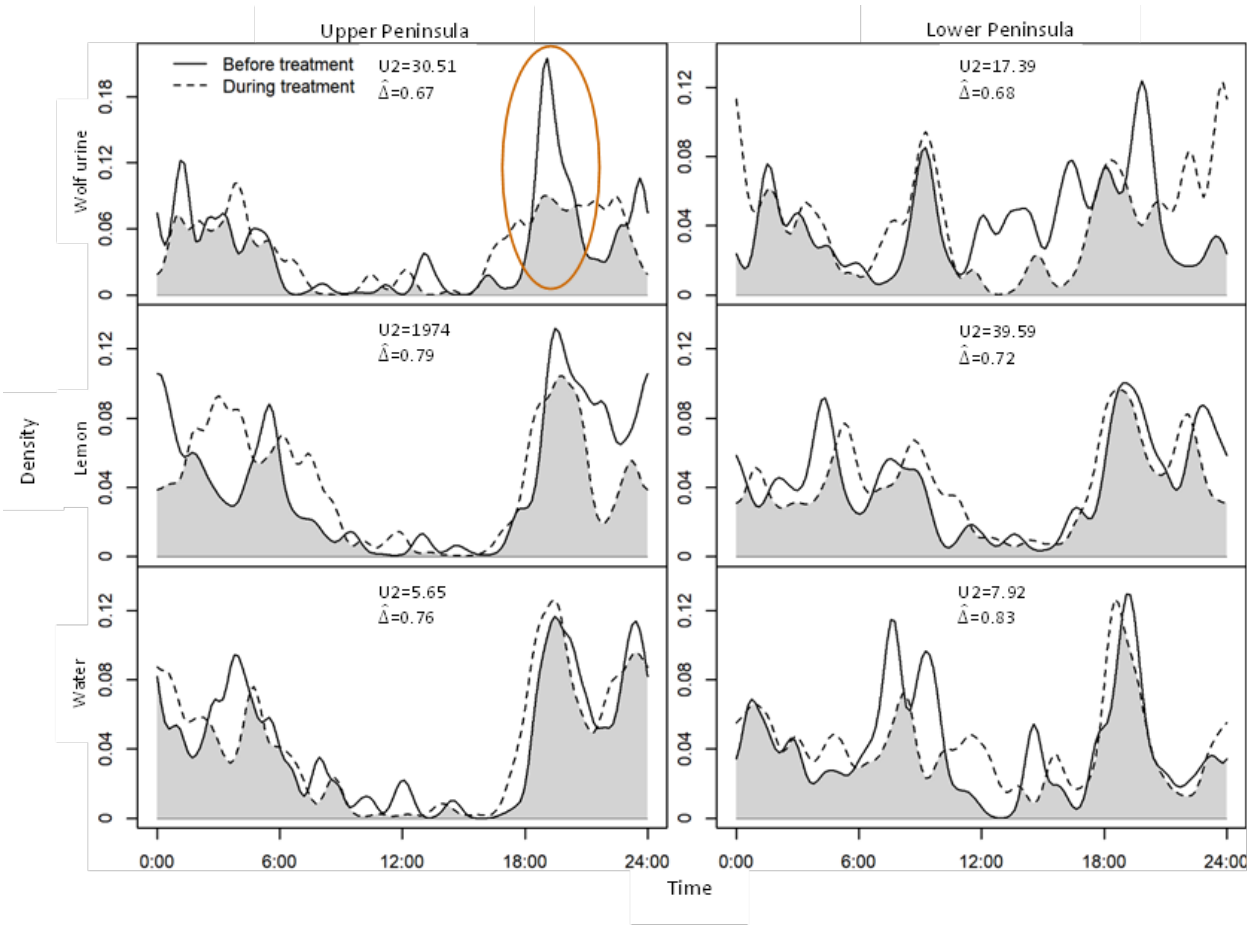

Upper Peninsula
Lower Peninsula
Before treatment
During treatment
U2=30.51
Δ̂=0.67
U2=17.39
Δ̂=0.68
U2=1974
Δ̂=0.79
U2=39.59
Δ̂=0.72
U2=5.65
Δ̂=0.76
U2=7.92
Δ̂=0.83
Wolf urine
Lemon
Water
Density
0:00
6:00
12:00
18:00
24:00
Time

Figure 4

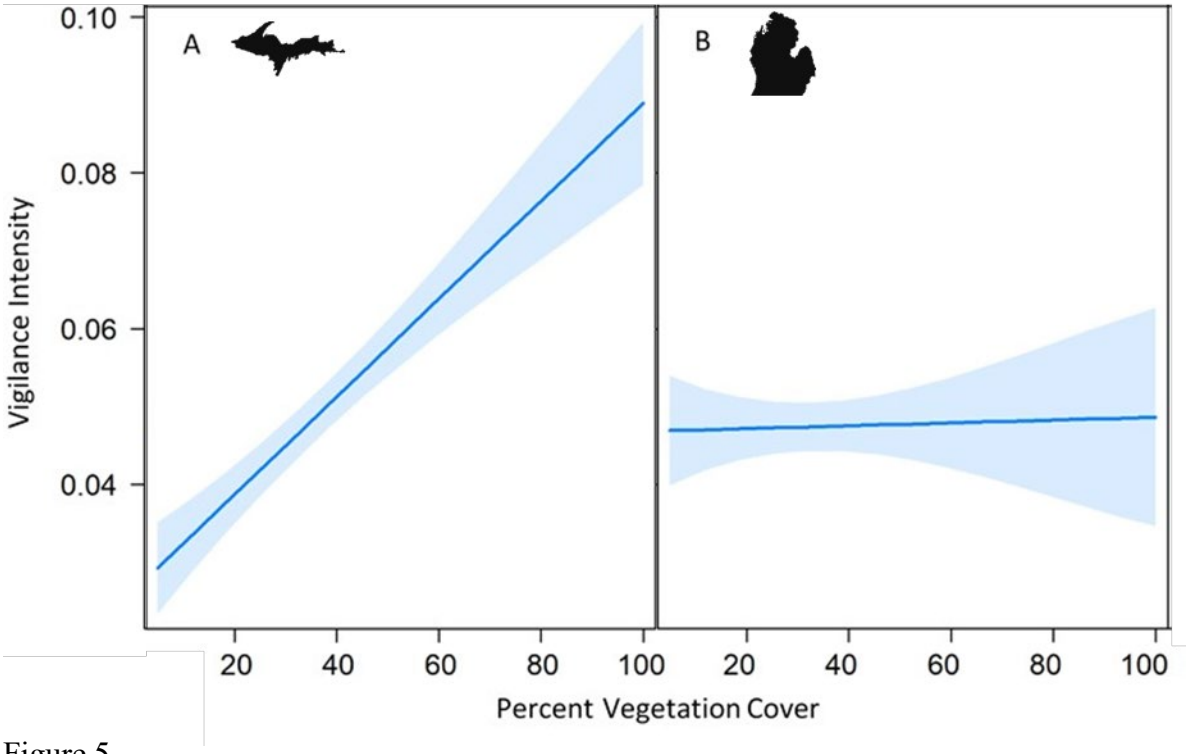

A
B
0.10
0.08
0.06
0.04
Vigilance Intensity
20
40
60
80
100
20
40
60
80
100
Percent Vegetation Cover

Figure 5