Reducing the potential for human-snake encounters in a recreational park

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Abstract: Parks and outdoor recreation areas often struggle to balance management for outdoor recreation with the protection of native flora and fauna. Additional complications can arise for land managers when recreation occurs in areas shared with wildlife that are perceived by humans to be dangerous. Despite these issues, many parks may inadvertently increase the potential for human—wildlife encounters through the creation of artificial forest gaps used for recreational purposes. We determined the potential for human encounters with venomous copperhead snakes (*Agkistrodon contortrix*) at a recreational park in southern Indiana before and after several simulated closures of recreational forest gaps. By restricting human access to artificial forest gaps, encounters with copperheads could be reduced by 1.5 to 8 times the observed encounter rate. We discuss conservation implications and provide suggestions for recreational park managers facing related concerns of human—wildlife encounters.

Key words: artificial gaps, conservation implications, copperhead, human–wildlife conflicts, human–wildlife encounters, management, outdoor recreation, park, venomous snakes

Losos et al. (1995) suggest that outdoor recreation is the second leading cause for the decline of federally threatened and endangered species on public lands. On the other hand, outdoor recreation provides a means to educate the public and increase its awareness of conservation issues, stimulate an appreciation of wildlife through opportunities to interact with nature, and generate revenue that may be applied to conservation management. Park managers may, thus, frequently encounter challenges regarding the balance of outdoor recreation with the protection of local flora and fauna.

Additional dilemmas can arise for park managers when recreation occurs in areas shared with wildlife perceived by humans to be dangerous. While the perceived danger may be exaggerated or misinterpreted in some cases, legitimate risk for visitors (bites, attacks, etc.) may indeed be present in others. If visitors are harmed, managers can face difficult decisions, as these encounters often lead to waves of negative publicity or temporary park closures. Consequently, some

visitors may be discouraged from enjoying the outdoors, and parks can face periods of decreased revenue (Knight and Temple 1995, Gore et al. 2005). Negative consequences can also exist for wildlife if they are persecuted, killed, or selectively transported, the last of which has questionable efficacy in preventing future encounters (Stahl et al. 2001). Even when encounters are nonthreatening to humans, persecution of wildlife may introduce a risk for both humans and wildlife that would otherwise not exist, as many animal attacks, particularly snake bites, are the result of provocation (Ernst and Zug 1996, Loe and Roskaft 2004, White and Gehrt 2009).

Despite these potential complications, recreation areas may sometimes inadvertently increase the potential for human-wildlife encounters. For example, artificial forest gaps often are created for recreational use in the form of hiking trails, overlooks, campsites, and picnic areas. These sites can provide an easy food source for many wildlife, and artificial gaps of any kind may become important thermoregulatory sites for ectotherms, such as snakes (Vitt et al. 1998, Greenberg 2001,

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Pringle et al. 2003). Risk for wildlife also can increase any time aggregations occur, and this risk may be especially high if populations are small and aggregations occur in close proximity to human activities.

Copperhead snakes (*Agkistrodon contortrix*; Figure 1) are one of the most widely distributed pit-vipers in the United States. Bites from this species are the second most common form of envenomation reported to the United States National Poison Center Database (Walker and Morrison 2011). While envenomation from a copperhead rarely is life-threatening, it can

cause severe pain, edema, and localized tissue death (Thorson et al. 2003). In this study, we describe a case study where artificial (recreational) forest gaps present potential management concerns for both humans and a declining population of copperhead snakes in a recreational park in southern Indiana. The potential for human–copperhead encounters is described, and the effectiveness of different simulated methods for reducing encounters is tested.

Methods

This study occurred from April 2009 to November 2011 at Clifty Falls State Park, a 573-ha recreational park in Jefferson County, southern Indiana. The park is characterized by a matrix of talus slopes and shallow canyons, primary and secondary deciduous upland areas, and approximately 30 ha of publicuse areas—including frequently used hiking trails—interspersed throughout. Park visitation is up to 500,000 people per year, with an estimated 60 individuals/ha/day within publicuse areas during summer (R. O. Davis, Park Naturalist, Indiana Department of Natural Resources, personal communication; Indiana Department of Natural Resources 2012).

We captured copperheads in suitable habitat by active search from late April to late May of each year and selected a subset of all snakes captured for surgical implantation of radiotransmitters (Holohil model SB-2T;



Figure 1. Copperhead snake (*Agkistrodon contortrix*; *photo by E. T. Carter*).

Holohil Systems Ltd., Carp, Ontario, Canada) based on size (transmitter ≤2.5% of snake mass) and sex (equal proportion of males, gravid females, and nongravid females). Surgical procedures were adapted from Reinert and Cundall (1982) using isoflurane as an anesthetic. Following a recovery period of 3 days, each snake was released at its original capture site and located 3 to 4 times per week throughout the primary activity season (May to October; Carter 2012). Latitude and longitude coordinates were recorded and later mapped in ArcMap 9.3 (Environmental Systems Resource Institute, Redlands, Calif., 2009).

We defined the potential for a human-copperhead encounter to occur if a copperhead was located within 3 m of a recreational trail or human-use site. We focused on locations during daylight hours, because at night access to the park is limited primarily to roads. Additionally, copperheads are largely nocturnal and remain sedentary during daylight while basking at the surface (Minton 2001, Carter 2012). Locations during daylight hours are, thus, better representative of where snakes are located throughout the day when human traffic is expected.

We considered human-use sites to be humanaltered forest gaps designed and maintained by park staff for recreational purposes. Two gaps within the study area fit these criteria, which we term the "tower" and "overlook." We assumed that both sites received equal volumes



Figure 2. Situated atop the southern extremity of a north-south running ridge, the area below the observation tower serves as a major gestation site for copperheads while receiving high levels of human traffic.

of human traffic, as they occur along the same 1.5-km trail. The tower consists of a 220-m² clearing surrounding a popular observation tower (Figure 2). It is situated at the southern extremity of a ridge running roughly northsouth and receives sun exposure throughout the day. The entire area is regularly padded with gravel, and both the center (directly below the tower) and periphery contain light weed growth. The overlook consists of a section of trail that passes over an old rock foundation (area 100 m²), which also is situated along a north-south oriented ridge. The foundation, which has primarily a western exposure, is approximately 1.5 m tall and 5 m long, with overlapping limestone rocks forming several crevices used by copperheads.

To assess the potential for human–copperhead encounters in recreational gaps before actual closure by park staff in 2010, we compared the frequency of observed and expected snake locations falling within 3 m of a trail or artificial forest gap. The expected number of locations occurring within 3 m of a trail or artificial forest gap was calculated as the total number of snake locations multiplied by the relative area of each habitat, including a 3-m buffer, within the study area (defined by a 40-m-buffered minimum convex polygon enclosing all snake locations). We then simulated the closure of each of these sites to human traffic in which snake locations within these sites would be >3 m from human access. To determine which closure scenarios resulted in lower potential for

human-copperhead encounters, we compared the frequency of snake locations within 3 m of a recreational trail or artificial forest gap before and after 4 separate treatments: no human-restricted access to the tower and overlook sites, restricted access to the tower only; restricted access to the overlook only; and restricted access to both the overlook and the tower combined.

Comparisons between treatments were carried out through the use of multiple chisquare analysis. We minimized type I error for multiple tests through Bonferroni corrections, report the adjusted P-values we (considered significant at $P \le 0.05$), herein. We selected chi-square analysis, as opposed to other statistical tests better suited to habitat use, because we were concerned only with the relative probability of an encounter occurring within each site rather than habitat preference by individual snakes. The probability that any human-snake encounter occurs in a given period is proportional to the number of locations-not individual snakes-within the vicinity of human-use sites if each snake is located at equal frequency and human traffic is consistent across sites (see Appendix 1 for an alternative analysis of daily encounter rate).

To determine whether telemetered snakes actually preferred artificial gaps over other available habitat at the landscape level, we used compositional analysis to compare proportional use of habitat by individual snakes to availability (Aebischer 1993). Because

recreational gaps were actually closed to the public after 2009 (but continued to be managed by intermittent hand removal of vegetation), we compared preference for these same sites before and after this closure. Individual snakes that were monitored for multiple years were not considered independent observations, with an exception being females that were monitored during both gravid and nongravid years (Reinert 1993, Minton 2001, Carter 2012). We used the AdehabitatHS Package (Calenge 2006) in R version 2.15.2 (R Core Team, Vienna, Austria, 2012) to perform the compositional analysis using randomization simulations to both rank and make pairwise comparisons between habitats.

Results

We obtained 394 locations of 11 snakes from May to October 2009 (preceding actual closure of artificial forest gaps by park staff) and an additional 780 locations of 17 snakes from May 2010 to November 2011 (following actual closure). Prior to actual closure of the tower

and overlook, recreational sites were in the following order of increasing daily probability of a potential human–copperhead encounter: hiking trail ($\bar{x}=0.065, 95\%$ CI = 0.038-0.103) < tower ($\bar{x}=0.190, 95\%$ CI = 0.135-0.260) \leq overlook ($\bar{x}=0.270, 95\%$ CI = 0.204-0.350; 95% CIs are based on 10,000 bootstrap replicates of 109 tracking days; see Appendix 1). The expected mean probability of encounter, based on 10,000 simulations, was significantly lower than the observed mean for each recreational site (hiking trail: 95% CI = 0.008–0.049, P=0.002; tower: 95% CI = 0.000–0.011, $P \leq 0.001$; overlook: 95% CI = 0.000–0.003, $P \leq 0.001$; Appendix 1; Figure A1).

Across the entire 2009 activity season, 54% of snake locations were situated within 3 m of a trail or artificial forest gap, whereas only 2.5% of locations were expected to occur within 3 m of a trail or artificial forest gap ($\chi_1^2 = 196.28$, $P \le 0.001$; Figure 3). As expected, not restricting access to both artificial forest gaps resulted in

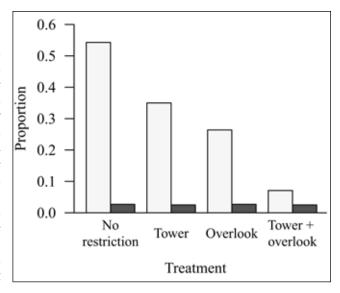


Figure 3. The potential for a human–copperhead encounter at Clifty Falls State Park, Jefferson County, Indiana, from May to October 2009. The proportion of snake locations within 3 m of a recreational trail or artificial forest gap during each of 4 simulated treatments: no restricted access, restricted access to the tower only, restricted access to the overlook only, and restricted access to both the tower and overlook. Light bars represent the observed number of snake locations (*n* = 394 locations from 4 males, 3 nongravid females, and 4 gravid females). Dark bars represent the expected number of locations. The proportion of locations expected to occur within 3 m of the tower, overlook, and tower plus overlook under no restricted access are all <0.01; thus, differences between the expected proportions in each restricted access treatment are nearly indiscernible in the figure.

the highest potential for human-copperhead encounters and was significantly greater than all other treatments (tower restriction: χ_1^2 = 28.8815, $P \le 0.001$; overlook restriction: $\chi_1^2 =$ 62.640, $P \le 0.001$; tower + overlook restriction: $\chi_1^2 = 204.109, P \le 0.001$; Figure 3). Restricting access to both the overlook and the area surrounding the tower resulted in lower potential for human-copperhead encounters when compared to restricting access to only the overlook ($\chi_1^2 = 51.18$, $P \le 0.001$) or the tower $(\chi_1^2 = 90.67, P \le 0.001)$. When having the option of restricting access to only 1 recreational site, closing the overlook would result in marginally for human-copperhead potential encounters $(\chi_1^2 = 6.46, P = 0.06; Figure 3).$ Each of these results was consistent when considering the daily probability of a humancopperhead encounter (2-sample permutation tests; Appendix 1, Figure A2).

Seven of the 11 telemetered copperheads utilized the overlook during 2009, and five

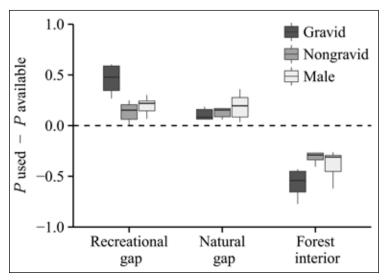


Figure 4. Index of habitat selection by radio-telemetered gravid female (black bars, n = 6), nongravid female (dark gray bars, n = 6), and male (light bars, n = 9) copperheads for recreational forest gap (tower, overlook, and hiking trail), natural forest gap, and forest interior at Clifty Falls State Park, Jefferson County, Indiana. Preference was consistent before and after actual closure of recreational gaps; thus, data were pooled across all years of the study (2009 to 2011). Index is proportion (P) of habitat used by individual snakes minus the proportion of habitat available at the landscape level. Boxes represent the interquartile range, solid horizontal lines represent medians, and error bars represent extreme values. Values above zero (dashed line) indicate preference, whereas values below zero indicate avoidance. Note that greater preference for recreational gap is driven primarily by gravid females.

of eleven utilized the tower during 2009 (including 3 males, 4 nongravid females, and 4 gravid females). We also recorded multiple observations of 3 unmarked adult copperheads (2 gravid females and 1 male) at the overlook and 1 unmarked adult copperhead (male) at the tower during 2009 in addition to several neonates. During the 2009 active season, 3 telemetered copperheads were observed at the overlook, and 2 telemetered copperheads were observed at the tower at any time. Not including neonates, the overlook contained ≤10 individuals, while the tower contained up to 6 individuals during a single observation.

Differences in habitat preference were revealed with compositional analysis before actual closure of recreational gaps by park staff ($\lambda = 0.069$, n = 11, P = 0.01) and following closure ($\lambda = 0.012$, n = 17, P = 0.002). However, preference did not change when considering only those individuals tracked both before and after closure (n = 7) or when considering all individuals tracked from 2009 to 2011 (n = 21). In all cases, habitats were ranked in the following order of increasing preference

by snakes: forest interior, natural gap, recreational gap (< indicates significant difference [P < 0.05] based on 10,000 randomization simulations. The index of habitat selection (proportion used minus proportion available) was positive for recreational and natural gap and negative for forest interior (Figure 4).

Discussion

Copperheads, like many ectotherms, are known to utilize forest gaps (Fitch 1960, Reinert 1984, Carter 2012) likely as a means to thermoregulate, and, within the park, copperheads utilize canopy gaps near public access (Figures 3 and 4). This is likely a result of these gaps being maintained by park staff, whereas gaps in the forest interior are

absent or facing successional growth owing largely to extensive exotic plant invasions (Carter 2012). Recreational use of artificial forest gaps presents unique management concerns and a potential risk for visitors and copperheads alike. For example, hikers are regularly observed hanging their legs over the edge of the overlook in close contact with crevices containing refuging or basking copperheads; adult and neonate copperheads have been intentionally killed at the tower and overlook sites on multiple occasions (Figure 5; (R. O. Davis, Indiana Department of Natural Resources, personal communication; Carter, unpublished data). Despite this potential contact, only one bite has been recorded within the park while several snakes are intentionally killed every year (R. O. Davis, Indiana Department of Natural Resources, personal communication; Carter, unpublished data)..

The potential for human-copperhead encounters could be reduced by closing either or both artificial gaps indicated in this study. Restricting access to the tower, overlook, or both would reduce encounters by 1.5, 2, or 8

x the baseline encounter rate (no restriction), respectively. Based park visitor logs calculated specifically the overlook for and tower trail system for each day in 2009, (Indiana Department of Natural Resources 2012; R. O. Davis, personal communication), these values translate average reductions from roughly 1,100 visitors encroaching on individual radiotelemetered snakes each day to roughly 730, 550, or 140, respectively (Figure 3; Appendix 1). While restricting access to

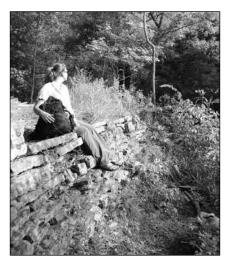


Figure 5. Hikers are regularly observed hanging their legs over the overlook in immediate proximity to refuging and basking copperheads, introducing potential risk for both snake and hiker.

both sites would provide the most substantial reduction in the potential for encounters, it may not be feasible for a park to implement multiple restrictions. Nonetheless, restricting access to either site in this study would still reduce potential encounters by tens of thousands each year.

In areas where sections of trail create gaps being utilized by wildlife, a trail itself may be moved rather than restricting access to entire areas. This can be effective by moving a trail by only a few meters or by creating raised walkways. For example, the section of trail running through the overlook was moved 3 m to the downhill edge of the ridge, effectively bypassing the overlook by traversing through habitat less preferable to copperheads. This scenario may be a highly desirable alternative for park managers and visitors, as visitors may still enjoy the scenic value offered without encroaching on wildlife or disturbing important habitat. This method has been gaining endorsement from nature preserves in our region, where human contact with nature is prohibited but observation is encouraged.

An alternative management practice might involve creating additional artificial gaps in the forest interior away from public access. The creation of artificial gaps in the forest interior would provide thermoregulatory opportunities for ectotherms (Vitt et al. 1998, Pringle et al. 2003,

Webb et al. 2005) and may decrease the potential for human-wildlife encounters by providing habitat away from human access. These situations also present opportunities for vital conservation research as the degree to which different species respond to such habitat manipulation and its long-term implications largely unknown (Shoemaker et al. 2009).

The selection of sites for the creation of artificial forest gaps should involve a thorough consideration of the habitat needs of any species involved. For instance, Pringle et al. (2003)

found that incident radiation was influenced predominantly by the location of canopy gaps in relation to the path of the sun; thus, the imperiled broad-headed snake (*Hoplocephalus bungaroides*) was restricted to canopy openings at the tops of west-facing cliffs. Accordingly, copperheads and other temperate-forest ectotherms are commonly believed to exhibit preference for gaps on or near south-facing slopes. However, this assumption does not always hold true even within populations (e.g., Smith 1996, Thomas et al. 1999). In our current example, copperheads appear to exhibit preference for gaps on southto-west-facing slopes, but preference differs slightly between sex and gravidity (Carter 2012; Figure 4). Thus, we suggest that artificial gaps be created in a number of situations to accommodate such potential differences and attempt to maximize their effectiveness across species and populations. For example, we created several artificial gaps of varying size, slope, and exposure that will continue to be monitored.

If additional artificial gaps are created or if suitable habitat exists elsewhere, wildlife may continue to utilize a closed site, particularly if breeding or foraging success was previously high in that location (Switzer 1997, Haas 1998, Porneluzi 2003). Both the tower and overlook serve as major gestation and parturition sites for copperheads. This is evidenced from the fact

that nearly all telemetered gravid females and several nontelemetered individuals selected one of these locations as their primary gestation site, and parturition has taken place at each of these sites during every year of the study (Carter 2012). Unfortunately, restricting access to any recreational site will typically translate to a site no longer being managed. A paradoxical situation may exist in that it is human use that maintains low levels of vegetation or other characteristics preferred by snakes, thereby creating the attractive habitat for wildlife in the first place. If sites are not managed following restriction, wildlife may continue to utilize an increasingly lower quality habitat.

Populations also can be highly vulnerable when aggregations occur in relatively few and small areas, and this risk can be greatly increased when the individuals using those sites are primarily gravid females, for example. Even greater risk may be present when those habitats are also subject to successional change or anthropogenic perturbations (e.g., Sadovy and Domeier 2005, Vepsäläinen et al. 2007). Considering each of these potential management concerns, particular care should be taken in determining the proper course of action whenever wildlife exhibit preference for, and potentially become dependent on, humanuse sites. If a decision is made to restrict access to any site, we recommend that low-impact management (e.g., intermittent hand removal of vegetation) continue where possible, at least until there is evidence that wildlife have transitioned into other suitable habitats that are less prone to human encroachment. Of course, any time seasonal patterns of habitat use within recreational sites are apparent, temporary closure may be a simpler and less costly strategy.

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Literature cited

- Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.
- Carter, E. T. 2012. Impacts of invasive plants on resource selection and thermoregulation by the northern opperhead (*Agkistrodon contortrix mokasen*). Thesis, Purdue University, West Lafayette, Indiana, USA.
- Ernst, C. H., and G. R. Zug. 1996. Snakes in question. Smithsonian Institution Press, Washington, D.C., USA.
- Fitch, H. S. 1960. Auteology of the copperhead. University of Kansas Publications, Museum of Natural History 13:85–288.
- Gore, M. L., W. F. Siemer, J. E. Shanahan, D. Scheufele, and D. J. Decker. 2005. Effects on risk perception of media coverage of a black bear-related human fatality. Wildlife Society Bulletin 33:507–516.
- Greenberg, C. H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecology and Management 148:134–144.
- Haas, C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk 115:929–936.
- Hothorn, T., and K. Hornik. 2013. exactRankTests: exact distributions for rank and permutation tests. R package version 0.8-27, http://CRAN.R-project.org/package=exactRankTests. Accessed April 30, 2014.
- Indiana Department of Natural Resources. 2012. State park and reservoirs visitation—fiscal year

- 2010. Indiana Department of Natural Resources, Division of Parks and Reservoirs, Indianapolis, Indiana, USA, http://www.in.gov/dnr/parklake/2441.htm. Accessed April 30, 2014.
- Knight, R. L., and S. A. Temple. 1995. Wildlife and recreationists: coexistence through management. Page 327–333 in R. L. Knight and K. J. Gutzwiller, editors. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C., USA.
- Loe, J., and E. Roskaft. 2004. Large carnivores and human safety: a review. AMBIO 33:283–288.
- Losos, E., J. Hayes, A. Phillips, D. Wilcove, and C. Alkire. 1995. Taxpayer-subsidized resource extraction harms species. BioScience 45:446– 455.
- Minton, S. A. 2001. Amphibians and reptiles of Indiana. Indiana Academy of Science. Indianapolis, Indiana, USA.
- Peng, R. D. 2008. simpleboot: simple Bootstrap routines. R package version 1.1-3.
- Porneluzi, P. A. 2003. Prior breeding success affects return rates of territorial male ovenbirds. Condor 105:73–79.
- Pringle, R. M., J. K. Webb, and R. Shine. 2003. Canopy structure, microclimate, and habitat selection by a nocturnal snake, *Hoplocephalus bungaroides*. Ecology 84:2668–2679.
- Reinert, H. K. 1984. Habitat variation within sympatric snake populations. Ecology 65:1673–1682.
- Reinert, H. K. 1993. Habitat selection in snakes. Pages 201–240 *in* R. A. Seigel and J. T. Collins, editors. Snakes: ecology and behavior. McGraw-Hill, New York, New York, USA.
- Reinert, H. K., and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. Copeia 1982:702–705.
- Sadovy, Y., and M. Domeier. 2005. Are aggregation-fisheries sustainable? reef fish fisheries as a case study. Coral Reefs 24:254–262.
- Shoemaker, K. T., G. Johnson, and K. A. Prior. 2009. Habitat manipulation as a viable conservation strategy. Pages 221–243 *in* S. J. Mullin and R. A. Seigel, editors. Snakes: ecology and conservation. Cornell University Press, Ithaca, New York, USA.
- Smith, G. R. 1996. Habitat use and its effect on body size distribution in a population of the tree lizard, *Urosaurus ornatus*. Journal of Herpetology 30:528–530.

- Stahl, P., J. M. Vandel, V. Herrenschmidt, and P. Migot. 2001. The effect of removing lynx in reducing attacks on sheep in the French Jura Mountains. Biological Conservation 101:15–22.
- Switzer, P. V. 1997. Past reproductive success affects future habitat selection. Behavioral Ecology and Sociobiology 40:307–312.
- Thomas, J. A., R. J. Rose, R. T. Clarke, C. D. Thomas, and N. R. Webb. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Functional Ecology 13:55–64.
- Thorson, A., E. J. Lavonas, A. M. Rouse, and W. P. Kerns. 2003. Copperhead envenomations in the Carolinas. Clinical Toxicology 41:29–35.
- Vepsäläinen, V., T. Pakkala, M. Picha, and J. Tiainen. 2007. The importance of breeding groups for territory occupancy in a declining population of a farmland passerine bird. Annales Zoologici Fennici 44:8–19.
- Vitt, L. J., T. C. S. Avila-Pires, J. P. Caldwell, and V. R. L. Oliveira. 1998. The impact of individual tree harvesting on thermal environments of lizards in Amazonian rain forest. Conservation Biology 12:654–664.
- Walker, J. P., and R. L. Morrison. 2011. Current management of copperhead snakebite. Journal of the American College of Surgeons 212:470–474.
- Webb, J. K., R. Shine, and R. M. Pringle. 2005. Canopy removal restores habitat quality for an endangered snake in a fire suppressed land-scape. Copeia 2005:894–900.
- White, L. A. and S. D. Gehrt. 2009. Coyote attacks on humans in the United States and Canada. Human Dimensions of Wildlife 14:419-432.

Appendix: 1

Simulating daily probability of humancopperhead encounters

To provide a more quantitative approach for demonstrating the potential for human-copperhead encounters in recreational sites, we calculated the number of individual snakes located within 3 m of a trail or human-use site for each day that we obtained snake locations prior to actual closure of the tower and overlook sites in 2010 (n = 109 tracking days). To

provide a null expectation, we used R version 2.15.2 to generate 10,000 random draws from a multinomial distribution for each day (R Core Team, 2012). Daily sample sizes were equal to the observed number of snake locations on each day, and expected probabilities of presence were equal to the relative size of each habitat type within the study area (minimum convex polygon enclosing all snake locations; humanuse sites included a 3-m buffer). We then converted both observed and expected counts to proportions for each day, thereby providing relative probabilities of occurrence within each site for each of 109 tracking days in 2009 (all individual snakes were located at equal frequency). Under the assumption that all sites receive equal volumes of human traffic (R. O. Davis, Park Naturalist, Indiana Department of Natural Resources, personal communication), probabilities of occurrence represent the relative probability of a potential human-copperhead encounter for any site receiving human traffic.

test the hypothesis that observed encounters were greater than expected at random, we compared the observed mean probability of encounter within each site to the corresponding null distribution of means. P-values were determined by calculating the n + 1 simulated means that were greater than or equal to the observed mean divided by the n + 1 simulations. We then multiplied this resulting probability by the number of pairwise comparisons (i.e., Bonferroni adjustments). To compare observed probability of encounter between sites, we conducted permutation tests using the exactRankTests package in R (Hothorn and Hornik 2013). We then simulated the closure of the overlook and tower sites to human traffic in which snake locations would be >3 m from human access. To determine whether restricting access to a particular site would result in lower potential for human-copperhead encounters, we again used permutation tests to compare the relative reduction in encounters in 4 separate treatments: no restricted access, restricted access to the tower only, restricted access to the overlook only, and restricted access to both the overlook and the tower combined.

We considered all tests to be significant at $P \le 0.05$, and all P-values are reported with Bonferroni adjustments applied. We also report

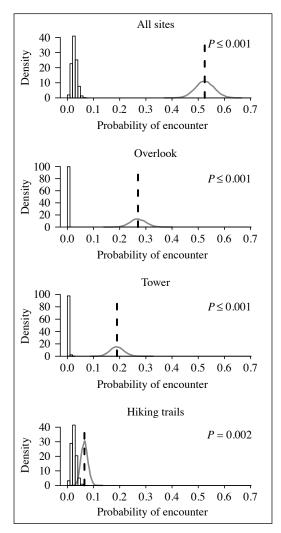


Figure A1. Probability densities of observed and expected mean daily probability of a potential human–copperhead encounter at Clifty Falls State Park, Indiana, for 109 radiotracking days in 2009. Histograms (vertical bars) represent null expectations of means across 10,000 simulations, which were compared to the single, observed mean for each site (dashed lines). Bonferroni-adjusted *P*-values are displayed within the plot for each comparison. Grey lines represent 10,000 resamples of observed values for each site. Each pairwise comparison between sites was also significant with the exception of the tower versus overlook (*P* = 0.064, 2-sample permutation test).

95% Bonferroni CIs for both observed resampled means and simulated means. Confidence intervals for resampled means were calculated according to the bootstrap bias-corrected and accelerated (BCa) interval method using the simpleboot package in R (Peng 2008).

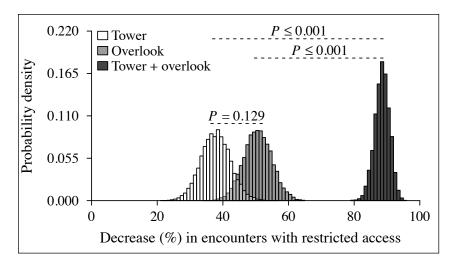


Figure A2. Mean percentage decrease in the potential for human–copperhead encounters (relative to no human-restricted access to any site) at Clifty Falls State Park, Indiana, in 4 separate treatments: no restricted human access to the tower and overlook sites (at x = 0), restricted human access to the tower only (white bars), restricted access to the overlook only (grey bars), and restricted access to the tower and overlook combined (dark bars). Each histogram represents the distribution of 10,000 resampled means. Bonferroni-adjusted P-values, based on 2 sample permutation tests, are displayed above dashed lines linking treatments. All comparisons to no restricted access were significant (tower restriction: P = 0.038, overlook restriction: $P \le 0.001$, tower + overlook restriction: $P \le 0.001$).

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