6-1-2017

Forecasting Disturbance Effects on Wildlife: Tolerance Does Not Mitigate Effects of Increased Recreation on Wild Lands

B. P. Pauli
Boise State University

R. J. Spaul
Boise State University

J. A. Heath
Boise State University

This is the peer reviewed version of the following article:
which has been published in final form at doi: 10.1111/acv.12308. This article may be used for non-commercial purposes in accordance with Wiley Terms and Conditions for Self-Archiving.
Forecasting Disturbance Effects on Wildlife: Tolerance Does Not Mitigate Effects of Increased Recreation on Wild Lands

Benjamin P. Pauli*
Department of Biological Sciences and Raptor Research Center
Boise State University
Boise, ID

Robert J. Spaul
Department of Biological Sciences and Raptor Research Center
Boise State University
Boise, ID

and

Julie A. Heath
Department of Biological Sciences and Raptor Research Center
Boise State University
Boise, ID

Corresponding author current address: Benjamin P. Pauli, Saint Mary's University of Minnesota, 700 Terrace Heights, Biology Dept., Box 10, Winona, MN 55987, Phone: 507-457-6681, Email: bpauli@smumn.edu

Abstract

There is widespread evidence that human disturbance affects wildlife behavior, but long-term population effects can be difficult to quantify. Individual-based models (IBMs) offer a way to assess population-level, aggregate effects of disturbance on wildlife. We created TRAILS (Tolerance in Raptors and the Associated Impacts of Leisure Sports), an IBM that simulates interactions between recreationists and nesting raptors, to assess the effect of human disturbance on raptor populations and test if changes in tolerance to disturbance could mitigate negative consequences. We used behavioral and demographic data from golden eagles (*Aquila chrysaetos*), and recreation activity data to parameterize TRAILS and simulate the effects of pedestrian and off-highway vehicle recreation on the likelihood of territory occupancy, egg-laying and nest survival of eagles over 100 years. We modeled eagle populations in the absence of recreation, with stationary 2014 levels of recreation, and with annual increases in recreation. Further, we simulated eagles that developed tolerance to disturbance randomly, through natural selection, habitat imprinting, or habituation. In the presence of recreation, simulated eagle populations had significantly lower and more variable growth rates, population sizes and territory occupancy. Annual increases in recreation of 1-2% greatly exacerbated population declines. Though both habituation and natural selection lead to more tolerant eagle populations, neither buffered eagle populations from detrimental effects of recreation. These results suggest that long-lived species that experience encroachment from human activities may not adapt to human disturbance at a rate that compensates for changes in disturbance. This project illustrates the usefulness of IBMs for evaluating non-lethal threats, forecasting population changes, and testing theoretical feedbacks in system processes.

Keywords: golden eagle; habituation; individual-based model; imprinting; sensitivity; tolerance

Introduction

Human disturbance of wildlife that results in an animal deviating from its normal behavior (Nisbet, 2000; Frid and Dill, 2002) has been of interest to conservation biologists for some time (Richardson and Miller, 1997). Human disturbance of wildlife causes animals to increase stress hormone concentrations (Busch and Hayward, 2009; Strasser and Heath, 2013), change habitat use (Andersen et al., 1990), expend greater energy (Arlettaz et al., 2014), reduce reproductive success (Müllner et al., 2004) and increase the probability of mortality (Wauters et al., 1997). Because
the compound effects of disturbance on individuals within an entire population can be complex, the population-level effects may not be readily apparent (Gill et al., 2001) and the long-term effect of disturbance on populations can be difficult to ascertain (King et al., 2015).

Individual-based models (IBMs) are simulation tools that capitalize on empirical research to examine scenarios that are difficult or impossible to study in a field setting. IBMs use information on individual animal behaviors (e.g., movements, mortality, reproduction) to simulate the interaction of many individuals. Population-level patterns emerge from the interaction of individuals with one another and their environment (Grimm and Railsback, 2005). Thus, IBMs are well suited for the investigation of the effects of disturbance on wildlife populations over long time frames (West and Caldow, 2006; Bennett et al., 2009).

One benefit of using simulation models is to forecast how changes in the environment or organisms and their behavior may affect populations. This is useful for understanding the effect of temporally dynamic recreation on wildlife (Duffus and Dearden, 1990). Also, wildlife tolerance of disturbance may change over time (Samia et al., 2015). Many wildlife species exhibit tolerance to human disturbance which may mask or mitigate long-term effects of disturbance (Nisbet, 2000; Baudains and Lloyd, 2007; Jiménez et al., 2013; Geffroy et al., 2015). Methods by which populations develop increased tolerance, however, may differ. Tolerance could increase due to the selective advantage of tolerant individuals if such traits were heritable (Lowry et al., 2011). Alternatively, habitat imprinting, whereby offspring select habitat similar to that of their natal experience (Davis and Stamps, 2004), could lead to more tolerant behavior (Guinn, 2013). Finally, habituation of individuals, the reduced response to a stimuli as the result of a lack of negative consequences, to human disturbance also could result in development of tolerance within a population (Bejder et al., 2009). Simulation models allow assessment of the role of tolerance in mitigating the effects of disturbance on wildlife, which itself may change over time.

The golden eagle (Aquila chrysaetos) is a long-lived, territorial species that occurs throughout much of the northern hemisphere. In the USA the golden eagle is federally protected under the Migratory Bird Treaty Act (16 U.S.C 703-712) and the Bald and Golden Eagle Protection Act (16 U.S.C. 668-668c) and, therefore, must be protected from human actions that negatively affect populations, including disturbance. Assessments of golden eagle populations in the western USA suggest stable or declining populations (Kochert and Steenhof, 2002; Hoffman and Smith, 2003; Millsap et al., 2013). In southwestern Idaho, breeding populations of golden eagles have been declining (Steenhof et al., 1997), and maintaining the quality of existing habitat has been deemed important to long-term population viability (Kochert et al., 2002).

Golden eagles are considered to be sensitive to human disturbance (Kochert and Steenhof, 2002; Whitfield et al., 2004). Human disturbance has been implicated in reduced eagle nesting productivity (Boeker and Ray, 1971). For example, eagles that experience high exposure to off-highway vehicles (OHVs) exhibit reduced productivity (Steenhof et al., 2014). In addition, motorized recreation activity caused decreased territory occupancy and nest survival, while non-motorized recreation (pedestrians, horseback riding, etc.) activity caused decreased probability of egg-laying in golden eagles (Spaul, 2015; Spaul and Heath, in review a). Therefore, maintaining habitat and populations in areas free from human disturbance is considered an important component of golden eagle conservation (Kochert and Steenhof, 2002).

Some raptor species show evidence of tolerance to human disturbance, which can change over time or with exposure to human activity. For example, red-tailed hawks (Buteo jamaicensis) were less sensitive to disturbance by helicopters in areas where flights regularly occurred (Andersen et al., 1989). Similarly, bald eagles (Haliaeetus leucocephalus) in Washington, USA showed decreased responses to boating and hiking in areas where such activities were common (Stalmaster and Newman, 1978; Knight and Knight, 1984). If golden eagles are able to develop tolerance to human disturbance, the potential exists for a population to change to mitigate the effects of recreation. Currently, little empirical research exists on the capacity for tolerance in golden eagle populations in response to disturbance.

The goal of this study was to develop an IBM to be used to examine population-level consequences of wildlife responses to recreation. We used empirical data on golden eagles and recreation in southwestern Idaho to parameterize the model. In addition, we explored whether tolerance to disturbance could mitigate the negative effects of recreation on eagles. We hypothesized that tolerance could become established in one of several ways: randomly, via directional
natural selection, habitat imprinting, or individual habituation. We predicted that in a long-lived species like golden eagles, tolerance gained through individual habituation would provide the greatest mitigation of disturbance effects as individuals could become increasingly tolerant over their lifetime.

**Materials and Methods**

We designed and coded the TRAILS (Tolerance in Raptors and the Associated Impacts of Leisure Sports) model in NetLogo (version 5.1.0, Wilensky, 1999; Appendix A). For a model description in overview, design concepts, and details (ODD) protocol (Grimm et al., 2006, 2010), please see Appendix A.

**Summary Model Description**

We designed TRAILS to assess the effect of recreation on raptor population dynamics (growth, size, and proportion of territories occupied) over a time scale that included multiple generations. Entities in TRAILS are composed of eagles, nests and matrix habitat. Eagles are the model agents, nests are characterized as a single grid cell in the landscape where eagles breed and the matrix habitat comprises the environment over which they behave. In reality, eagle territories can have several nests (Beecham and Kochert, 1975) but in TRAILS there is one nest per territory. Nests contain categorical and numerical variables associated with their availability, and recreation activity (Table 1). All nest-associated variables correspond to data from actual eagle territories in southwestern Idaho (Spaul, 2015; Spaul and Heath, in review a). Each virtual nest keeps track of its probability of occupancy by simulated eagles, whether it is occupied by a pair of eagles or whether it is available for a new pair to occupy it. Eagles are the only agents within TRAILS and are characterized by a number of state variables (Table 1). The simulated landscape is comprised of a 201 X 201 grid of cells, each cell representing ~0.25 km² in the “real world”, and represents a 100 X 100 km study site. There is no habitat type associated with the model. Cells that are not nests are treated identically as ‘matrix’ habitat.

Timesteps represent 1 day, in a 190-day breeding season. At the end of each breeding season, a single timestep occurs for winter, and the breeding season begins again immediately. During the winter, annual mortality occurs. Mortality rates are the same for all juveniles of the same age (Table 2). For adults under scenarios when tolerance is implemented, the mortality probability is the sum of the base mortality level and an additive value scaled by tolerance. The increased mortality cost of tolerance represents the cost associated with being in close contact with humans because eagles continue to suffer from direct persecution (Russell and Franson, 2014). For instance, if the additional mortality is a maximum of 2%, a maximally tolerant eagle will have a 2% greater mortality probability than a completely non-tolerant individual. The mortality rates for individuals between these extremes are linear. The model assumes territory fidelity and paired eagles remain on territories over subsequent years unless their mate dies or the level of OHV activity exceeds their tolerance. Each nest’s occupancy probability is determined during the winter. If the tolerance levels of either eagle on a nest precludes them from occupying that nest, both eagles will leave and attempt to pair and establish elsewhere.

In each timestep of the breeding season, the daily OHV level is calculated at each nest. Unpaired eagles attempt to pair, with males selecting empty nests and females selecting unpaired males with nests. The probability of a nest becoming occupied is influenced by the breeding season OHV level of the territory (Spaul and Heath, in review a). If no nests are available eagles become floaters and move randomly until a nest or mate becomes available.

Once eagles are paired, the likelihood of egg-laying is influenced by the early-season pedestrian activity in the territory (Spaul and Heath, in review a). Each pair can lay one or two eggs (potentially becoming 1 or 2 nestlings). The model does not account for imperfect hatchability or brood reduction. Eagle offspring may be of either sex and the tolerance of offspring can be randomly assigned, inherited from the mother or imprinted based upon the natal nest characteristics. Eggs that reach 45 days old turn into nestlings. During the egg and nestling stages, entire clutches/broods are subject to mortality based on nest-specific OHV activity and adult tolerance. When nestlings reach 63 days, they fledge into juveniles and, if habituation is enabled in TRAILS, the tolerance of the adult pair can increase. Juveniles remain out of the breeding population for 4 years and become adult eagles at 5 years old.
In TRAILS, the probability that young fledge is based on the compound probabilities of a nest being occupied, a pair laying eggs, and an egg/nestling surviving the incubation/brood-rearing stages. It is assumed that these probabilities are affected by recreation activity at nests. TRAILS is built on the concepts of tolerance whereby individuals are more or less sensitive to human disturbance, tolerance can change over time, and experiences as nestlings can influence tolerance (Davis and Stamps, 2004; Bejder et al., 2009).

Several population-level properties emerge from the interaction of eagles and the environment. The population growth rate, population size and territory occupancy at the end of the simulation are emergent properties. Also, the time to population extinction and the average tolerance of the population emerge from model behavior. Other patterns that emerge include: the average age at death of eagles, the mean number of young produced by the population per year, the mean number of young per pair, the mean number of eggs per pair, the mean success rate of eagle pairs and the mean proportion of successful territories.

Model Application

We compared model output under the base scenario (Table 2) to known empirical patterns of golden eagle ecology to assess the ability of TRAILS to capture the fundamental drivers of system dynamics (Wiegand et al., 2003; Grimm et al., 2005) and assessed the sensitivity of the model to individual parameters. In the base scenario, recreation existed at 2014 levels and did not increase over time. The model matched observed patterns of territory occupancy rates, productivity and relative population stability observed within the broader southwestern Idaho golden eagle population (Steenhof et al., 1997; Millsap et al., 2013). For details on the pattern matching procedure or sensitivity analyses, see the corresponding TRACE (TRAnsparent and Comprehensive Ecological modeling) documentation (Augusiak et al., 2014; Grimm et al., 2014; Appendix A).

We ran 35,000 simulations to investigate the effect of recreation, and the effects of changes in recreation and tolerance over time on eagles. Model scenarios consisted of all combinations of 1) recreation (on/off), 2) method of tolerance establishment (no tolerance, random, inheritance, imprinting, habituation), and 3) annual recreation activity change (0-3% in increments of 0.5%). Together, these parameter combinations resulted in 70 scenarios. Changes in recreation were a measure of the constant, compound increase in recreation annually. For example, in a scenario in which annual recreation change was set at 1%, each simulated year the level of OHV recreationists, pedestrian recreationists, and trail densities would increase by 1% over the prior year. Because of the stochastic nature of TRAILS, each scenario was replicated 500 times. We compared model output under varying scenarios using Welch’s t-tests and ANOVA tests using program R (version 3.1.3; R Core Team, 2015). Confidence intervals were calculated using the 2.5% and 97.5% quantiles of sample data. However, because classical hypothesis testing statistics may be misleading with simulated data (White et al., 2013), we focused on general trends and effect size of parameterization rather than statistical significance.

Results

Relative to a scenario with no recreation, 2014 levels of recreation significantly affected population growth ($t_{522} = 22.8, p < 0.00001$; Figure 1A), population size ($t_{652} = 42.1, p < 0.00001$; Figure 1B) and final territory occupancy ($t_{528} = 28.0, p < 0.00001$; Figure 1C). Simulations without recreation had higher population growth rates (without recreation – mean = 1.0069, 95% CI = 1.0045-1.0089; with recreation – mean = 0.9994, 95% CI = 0.9818-1.0056), population sizes (without recreation – mean = 131.24, 95% CI = 106.48-158.00; with recreation – mean = 72.94, 95% CI = 8.45-110.55) and final territory occupancy (without recreation – mean = 0.95, 95% CI = 0.84-1.00; with recreation – mean = 0.64, 95% CI = 0.08-0.92). In addition, the variance around model output was greater for simulations with recreation than without. The ratios of variance for simulations without recreation to those with recreation for population growth, population size and territory occupancy were 41.8, 5.2 and 33.5, respectively. Without recreation, the average population growth was always positive, but with recreation, populations declined in 32.4% of simulations. Similarly, without recreation, eagle populations always persisted for 100 years and with 2014 levels of recreation, eagle populations went extinct in under 100 years in 0.8% of simulations.

For scenarios in which recreation activity increased annually under varying degrees, the effects of disturbance on eagles significantly impacted population growth ($F_{6,3382} = 897, p < 0.00001$; Figure 2A), time to local extinction ($F_{6,3382} = 121, p < 0.00001$; Figure 2B), final population size ($F_{6,3382} = 1285, p < 0.00001$; Figure 2C) and final territory occupancy ($F_{6,3382} = 1166, p < 0.00001$; Figure 2D). These effects scaled with the increases in recreation (Figure 2).
As recreation levels increased the population growth rates of eagles became increasingly negative, the number of simulations with local extinction within 100 years increased, population sizes decreased and territory occupancy approached 0. Similar trends were observed under scenarios with varying tolerance mechanisms as well (Appendix B, Figures B1-B5).

When tolerance, in any form, was included in simulations recreation had less negative effects on populations (Appendix B, Figures B1-B5). Populations showed higher growth rates, fewer extinction events, greater population size and more territory occupancy. The mitigating effects of tolerance were greater when the mechanism for acquiring tolerance was through genetic inheritance or habituation rather than habitat imprinting or random assignment (Figure 3).

The mode of tolerance acquisition significantly affected population growth ($F_{4,2459} = 263, p < 0.00001$; Figure 3A), time to local extinction ($F_{4,2459} = 21, p < 0.00001$; Figure 3B), final population size ($F_{4,2459} = 332, p < 0.00001$; Figure 3C), final territory occupancy ($F_{4,2459} = 300, p < 0.00001$; Figure 3D) and population tolerance ($F_{4,2279} = 212, p < 0.00001$; Figure 3E) when recreation increased 2% annually. Interestingly, while population growth, territory occupancy and population size of inherited tolerance and habituation were similar at moderate levels of recreational increase (e.g., 2%), habituation resulted in less tolerant overall population compared to the inheritance mechanism (Figure 3E).

**Discussion**

Our results demonstrate that human disturbance via recreation can have dramatic and long-lasting effects on golden eagle populations. Simulated populations without the influence of disturbance from recreation had robust populations that exhibited population growth and nearly saturated territory occupancy. When recreation occurred at 2014 levels, however, eagle population abundances were lower and eagles occupied fewer territories compared to when recreation was absent. In addition, the variance associated with model predictions was greater in scenarios that included recreation. In the presence of recreation, populations frequently remained stable but occasionally displayed significant population declines. These results suggest that the effects of disturbance from recreation were not deterministic but were subject to stochasticity associated with eagle behavior. Empirical research has suggested that golden eagles behaviorally respond to human activity (Martin et al., 2009). For example, golden eagles have been shown to flush in response to normal human activity (Holmes et al., 1993) and recreation activity (Spaul and Heath, in review b). In addition, territory occupancy was shown to decline in response to increased human activity in Finland (Kaisanlahti-Jokimaki et al., 2008). Our modeling results suggest that human disturbance from recreation can have long-term, population-level effects on golden eagles.

Outdoor recreation across the US is increasing and is projected to increase in coming decades (Cordell et al., 2009; Bowker et al., 2012) and recreational use of golden eagle habitat has also increased and is expected to continue to increase (Steenhof et al., 2014). These results demonstrated that if such an increase occurred without significant management action to control disturbance, there would be negative effects on eagle populations. For instance, just a 1% annual increase in recreation resulted in negative population growth rates and substantially decreased eagle population size compared to no annual increases in recreation. Furthermore, a 3% annual increase in recreation resulted in the local extinction of eagles within 100 years in most simulations. Thus, even moderate growth in recreation activity can have major consequences on eagle populations. It should be noted, however, that recreation changes in our simulations consisted of equal increases in OHV recreation, pedestrian recreation and trail density. It is possible that these measures of recreation activity could grow disproportionately in the future and that this disproportionate growth could have varying impacts on golden eagle population dynamics. Future investigations that explicitly simulate such scenarios could help reveal the effects of such changes in recreation.

Our results suggested that tolerance to disturbance may not develop within a population at a sufficient rate to offset the effects of increasing recreation on breeding golden eagles. These simulations illustrated that tolerance, particularly when acquired via inheritance or habituation, increased over time and decreased the effects of recreation. However, no mechanism for tolerance resulted in an eagle population that was able to withstand even moderate recreational increases over time. Although some species may exist in human-dominated landscapes by becoming tolerant to human activities, a long-lived species with low recruitment, such as golden eagles, may be unable to experience individual
learning or population-level adaptation at a rate sufficient to compensate for a rapidly shifting anthropogenic landscape. Thus, trail management and a reduction of recreation activity within eagle territories will be necessary to maintain golden eagle populations in southwestern Idaho and other locations where recreation is increasing.

Interestingly, of the tested mechanisms for acquiring tolerance, results suggested that heritable tolerance may lead to population changes that effectively mitigate some human disturbance effects. Given that golden eagles have low productivity this result was surprising and suggests that recreation may be a strong selective force. In addition, habituation through individual ‘learning’ lead to increased tolerance of recreation. This result was less surprising because eagles are long-lived there may be potential for habituation to accumulate incrementally for eagles nesting in human-impacted areas. However, habituation is a ‘targeted’ process in that only individuals exposed to human disturbance are affected rather than the population as a whole. Therefore, only eagles in human-impacted territories become tolerant of disturbance, rather than the entire population.

Despite offering the most promise for natural mitigation of disturbance, our results suggested that even habituation may not be able to act at a rate sufficient to offset the effects of human disturbance if recreation activity continues to increase. It is important to note, however, that the implementation of tolerance in this model was relatively simple and constructed from a theoretical rather than empirical framework. The mechanism and degree of habituation in golden eagles is currently unknown. It is possible that eagle habituation occurs at a greater magnitude than we simulated and, therefore, may be better at mitigating the effects of disturbance than in these results. Furthermore, eagles may differentially develop tolerance to different recreation types. For instance, golden eagles may be more likely to become tolerant to the predictable nature of OHV recreationists moving quickly along trails than to pedestrians that move more slowly and may leave trails more readily (Spaul, 2015; Spaul and Heath, in review b). Additionally, it is possible that multiple mechanisms of tolerance work simultaneously and in concert with one another, thus increasing the ability of a population to mitigate the effects of disturbance.

Taken together, these results suggest that human disturbance via recreation activity has a substantial effect on golden eagle populations and that increasing recreation activity will exacerbate such effects. It should be noted that population dynamics of eagles in these simulations was primarily driven by human disturbance rather than other factors such as disease, diet or direct persecution, each of which could exacerbate the effects observed in this research. Other raptor species susceptible to disturbance from recreation may suffer population-level effects as well, and similar analyses should be undertaken on those species. Our research on golden eagles could serve as a template for other research on human disturbance of raptors and TRAILS itself could be modified for other species in other systems. Additionally, TRAILS could be used to test the implications of overall reductions in recreation activity or, though not currently implemented, be modified in such a way as to directly test the effect of trail placement on human disturbance of wildlife as has been done with other IBMs (Bennett et al., 2009). As we gain a greater understanding of the effects of disturbance on wildlife, individual-based modeling offers a valuable tool to recreation and wildlife managers to improve understanding of the long-term, population-scale influences of recreation on wildlife species.

Acknowledgements

This research was supported by the NSF Idaho EPSCoR Program and by the National Science Foundation under award number IIA-1301792, the Raptor Research Center and Department of Biological Sciences at Boise State University, the Bureau of Land Management and the USFWS Western Golden Eagle Team. Computing resources for this material is based in part upon work supported by the National Science Foundation under Grant No. 1229709. We are grateful for discussions with J. Sutter and B. Jost about recreation on public lands and wildlife management. K. Steenhof provided valuable feedback on an earlier version of this manuscript.
References


Table 1. State variables of simulated golden eagles and nests.

<table>
<thead>
<tr>
<th>Eagle State Variable</th>
<th>Description and possible values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupancy-status?</td>
<td>True = Eagle has a territory, False = no territory</td>
</tr>
<tr>
<td>Paired?</td>
<td>True = Eagle has a mate, False = no mate</td>
</tr>
<tr>
<td>Territory-nest</td>
<td>Eagle’s individual nest site</td>
</tr>
<tr>
<td>Mate</td>
<td>Eagles’ mate</td>
</tr>
<tr>
<td>Sex</td>
<td>Male or Female</td>
</tr>
<tr>
<td>My-age</td>
<td>Each eagles’ age, in days</td>
</tr>
<tr>
<td>Incubating?</td>
<td>True = Female is incubating, False = not incubating</td>
</tr>
<tr>
<td>Provisioning?</td>
<td>True = Female or male is currently tending a nest, False = is not</td>
</tr>
<tr>
<td>Already-tried?</td>
<td>True = Attempted breeding this season, False = did not</td>
</tr>
<tr>
<td>Success?</td>
<td>True = Successfully bred this season, False = did not</td>
</tr>
<tr>
<td>Floater?</td>
<td>True = Adult, non-territorial eagle False =Territorial adult</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>Eagle sensitivity to disturbance from 0 (tolerant) to 1 (intolerant)</td>
</tr>
<tr>
<td>Color</td>
<td>Brown = unpaired adult, blue = paired male, yellow = paired female, white = egg/nestling, black = juvenile</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nest State Variable</th>
<th>Description and possible values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupied?</td>
<td>True = Nest occupied by eagles, False = not occupied</td>
</tr>
<tr>
<td>Occ-prob</td>
<td>Probability of nest being occupied</td>
</tr>
<tr>
<td>Rec-generic</td>
<td>Breeding season OHV level of nest from (0.01 - 3.56)</td>
</tr>
<tr>
<td>Trail-density</td>
<td>Recreation trail and road density within 3 km of the nest (0.71 - 7.82)</td>
</tr>
<tr>
<td>OHV-vol</td>
<td>Breeding season OHV level of nest starting from (0.01 - 3.56; can change over time)</td>
</tr>
<tr>
<td>Ped-vol</td>
<td>Early-season pedestrian level of nest from (0.01 - 3.48)</td>
</tr>
<tr>
<td>OHV-vol-list</td>
<td>List of the last 9 days of OHVs per trail per day, occurring within 1200 m of nest</td>
</tr>
</tbody>
</table>
Table 2. Baseline values for parameters of individual-based model of golden eagle disturbance by recreationists in southwestern Idaho. For parameters that varied in different scenarios, all possible values of that parameter are included in brackets following the citation(s).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Citation(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Annual adult mortality</td>
<td>0.02</td>
<td>Calibrated from (Harmata, 2002; Hunt, 2002; Whitfield et al., 2004) (see Appendix A)</td>
</tr>
<tr>
<td>Juvenile mortality year 1</td>
<td>0.16</td>
<td>(Hunt, 2002; McIntyre et al., 2006)</td>
</tr>
<tr>
<td>Juvenile mortality year 2</td>
<td>0.21</td>
<td>(Hunt, 2002; Whitfield et al., 2004)</td>
</tr>
<tr>
<td>Juvenile mortality year 3</td>
<td>0.21</td>
<td>(Hunt, 2002; Whitfield et al., 2004)</td>
</tr>
<tr>
<td>Juvenile mortality year 4</td>
<td>0.21</td>
<td>(Hunt, 2002; Whitfield et al., 2004)</td>
</tr>
<tr>
<td>Max. mortality cost of tolerance</td>
<td>0.02</td>
<td>Theoretical. Modified from (Whitfield et al., 2004)</td>
</tr>
<tr>
<td>Degree of habituation change</td>
<td>0.40</td>
<td>Theoretical</td>
</tr>
<tr>
<td>Buffer in habitat imprinting</td>
<td>0.40</td>
<td>Theoretical</td>
</tr>
<tr>
<td>Recreation</td>
<td>On</td>
<td>N/A [On, Off]</td>
</tr>
<tr>
<td>Annual recreation growth</td>
<td>0%</td>
<td>N/A [0.0%, 0.5%, 1.0%, 1.5%, 2.0%, 2.5%, 3.0%]</td>
</tr>
<tr>
<td>Tolerance</td>
<td>Off</td>
<td>N/A [Off, Random, Inherited, Imprinted, Habituated]</td>
</tr>
<tr>
<td>Simulation years</td>
<td>100</td>
<td>N/A</td>
</tr>
</tbody>
</table>

**Figure Captions**

**Figure 1.** The population dynamics of a simulated golden eagle population with and without the effect of recreation. Panels depict the A) population growth rate, B) final population size (after 100 years) and C) final territory occupancy (following 100 simulated years).

**Figure 2.** The effects of increasing recreation activity on a golden eagle population. Panels depict the A) population growth rate, B) time to local extinction, C) final population size (after 100 years) and C) final territory occupancy (following 100 simulated years). Scenarios range from 2014 levels of recreation (0 annual change in recreation) to a 3% annual increase (0.03 annual change in recreation).

**Figure 3.** The potential for tolerance to human disturbance by golden eagles. Panels depict the A) population growth rate, B) time to local extinction, C) final population size (after 100 years) D) final territory occupancy (following 100 simulated years) and E) mean population tolerance under a 2% annual increase in recreation activity. Scenarios reflect varying ways in which simulated eagles develop tolerance: no tolerance (No tol.), randomly assigned (Random), genetically transferred (Inherit), habitat imprinting (Imprint) or through habituation (Habitate).
Figure 1
Figure 2
Figure 3
Appendix A: TRACE document

This is a TRACE document (“TRAnsparent and Comprehensive model Evaluation”) which provides supporting evidence that our model presented in:


was thoughtfully designed, correctly implemented, thoroughly tested, well understood, and appropriately used for its intended purpose.

The rationale of this document follows:


and uses the updated standard terminology and document structure in:


and


Contents

Problem formulation .................................................................................................................................................. 14
Model description .................................................................................................................................................. 15
Data evaluation .................................................................................................................................................... 20
Conceptual model evaluation ............................................................................................................................. 21
Implementation verification .................................................................................................................................. 22
Model output verification .................................................................................................................................... 23
Model analysis .................................................................................................................................................... 23
Model output corroboration ............................................................................................................................... 24
Literature cited ..................................................................................................................................................... 25
Figures ............................................................................................................................................................... 26

Problem formulation

This TRACE element provides supporting information on: The decision-making context in which the model will be used; the types of model clients or stakeholders addressed; a precise specification of the question(s) that should be answered with the model, including a specification of necessary model outputs; and a statement of the domain of applicability of the model, including the extent of acceptable extrapolations.
Summary

Golden eagles (*Aquila chrysaetos*) are a federally protected species that are also valued by viewers of wildlife. Other recreational activities, such as off-highway vehicle use or recreational hiking, negatively impact reproduction, but long-term impacts to populations are unclear. The goal of this model is to determine the effect of current and future recreational use on golden eagle populations. In addition, this model assesses the potential for eagle tolerance/habituation to offset the negative impacts of recreation. This model may be used by managers of golden eagle habitat to assess potential impacts of recreational use of public lands and set policy that may allow for the coexistence of eagles and recreationists.

This model describes the potential effects of recreational disturbance on nesting eagle populations in southwest Idaho. This model capitalizes on empirical information on the disturbance of nesting eagles by motorized and non-motorized recreationists within the Owyhee front. This model examines 1) Whether existing levels of recreational disturbance have significant influences on the population dynamics of golden eagles in Idaho? 2) What effect changing recreational pressure has on golden eagles? and 3) Can tolerance to recreational disturbance (derived randomly, inherited genetically, imprinted by natal site, or habituated over time) influence population dynamics and offset the costs of recreational disturbance? Tolerance is defined as individual variation in responsiveness to disturbance (Nisbet 2000, Bejder et al. 2009). Model output includes population growth rates, population size after a specified period of time, nest occupancy over time and the time to local population extinction (when applicable). In addition, the tolerance of the eagle population to recreational disturbance is tracked. These outputs offer the potential to examine the role recreational disturbance plays in eagle populations currently and into the future and may provide guidance for managers of eagle habitat on public lands for ways to manage recreational activities so that coexistence between eagle populations and human recreationists may be achieved.

Model description

This TRACE element provides supporting information on: The model. Provide a detailed written model description. For individual/agent-based and other simulation models, the ODD protocol is recommended as standard format. For complex submodels it should include concise explanations of the underlying rationale. Model users should learn what the model is, how it works, and what guided its design.

Summary

Below is a complete model description of the individual-based model of golden eagle population dynamics in response to recreational disturbance described using the ODD protocol.

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing individual-based models (Grimm et al. 2006, 2010). This model was written in NetLogo 5.1 (Wilensky 1999).

Purpose

We designed TRAILS to assess the effect of recreation on raptor population dynamics over a time scale that included multiple generations. TRAILS aimed to investigate three main questions: 1) Do existing levels of recreation influence the population dynamics (population growth, population size, and proportion of territories occupied) of golden eagles in southwestern Idaho? 2) What effect does changing recreation activity have on golden eagle populations? 3) Can tolerance to human disturbance, derived randomly, inherited genetically, imprinted by natal site, or individual habituation over time, influence population dynamics and offset the effects of recreation?
Entities, State Variables and Scales

Entities in TRAILS are composed of eagles, nests and matrix habitat. Eagles are the model agents, nests are characterized as a single grid cell in the landscape where eagles breed and the matrix habitat comprises the environment over which they behave. In reality, eagle territories can have several nests (Beecham and Kochert 1975) but in TRAILS there is one nest per territory and the terms nest and territory are used interchangeably.

Nests – Nests contain categorical and numerical variables associated with their availability, and recreation activity. Each nest is described by its early-season pedestrian level, breeding-season OHV level, recreation trail and road density within 3 km of the nest, and a running average of the last nine days of OHVs per trail per day, occurring within 1200 m of the nest. Previous research indicated these time scale and recreation activities were the most predictive of eagle breeding behavior and reproductive outcome in 2013 and 2014 (Spaul 2015, Spaul and Heath in review). All nest-associated variables correspond to data from actual eagle territories in southwestern Idaho (Spaul 2015, Spaul and Heath in review). Each virtual nest keeps track of its probability of occupancy by simulated eagles, whether it is occupied by a pair of eagles or whether it is available for a new pair to occupy it.

Eagles – Eagles are the only agents within the model and are characterized by a number of state variables (Table A1).

<table>
<thead>
<tr>
<th>State Variable</th>
<th>T = True, F = False</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupancy-status?</td>
<td>T = Eagle has a territory, F = no territory</td>
</tr>
<tr>
<td>Paired?</td>
<td>T = Eagle has a mate, F = no mate</td>
</tr>
<tr>
<td>Territory-nest</td>
<td>Each eagle pairs’ individual nest site</td>
</tr>
<tr>
<td>Mate</td>
<td>Each eagles’ mate</td>
</tr>
<tr>
<td>Sex</td>
<td>Male or Female</td>
</tr>
<tr>
<td>My-age</td>
<td>Each eagles’ age, in days</td>
</tr>
<tr>
<td>Incubating?</td>
<td>T = Female is incubating, F = not incubating</td>
</tr>
<tr>
<td>Provisioning?</td>
<td>T = Female or male is currently tending a nest, F = is not</td>
</tr>
<tr>
<td>Already-tried?</td>
<td>T = Attempted breeding this season, F = did not</td>
</tr>
<tr>
<td>Success?</td>
<td>T = Successfully bred this season, F = did not</td>
</tr>
<tr>
<td>Floater?</td>
<td>T = Adult, non-territorial eagle F = Territorial adult</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>Value between 0-1 (inverse of tolerance)</td>
</tr>
<tr>
<td>Color</td>
<td>Brown, blue, yellow, white, black</td>
</tr>
</tbody>
</table>

Table A1. State variables for each eagle in the model.

Environment – The simulated landscape is comprised of a 201 X 201 grid of cells, each cell representing ~0.25 km2 in the “real world”, and represents a 100 X 100 km study site. There is no habitat type associated with the model. Cells that are not nests are treated identically as ‘matrix’ habitat.

Process Overview and Scheduling

Timesteps represent 1 day, in a breeding season that lasts 190 days, from January 1-July 9. Each day is either a midweek day or a weekend day based upon a typical weekly calendar, and “Julian Week” is tracked for use in submodels which predict recreation volume. At the end of each breeding season, a single timestep occurs for winter, and the breeding season begins again immediately.

During the interbreeding season, annual mortality occurs and eagles that die are removed from the simulation. Annual mortality is the same for all juveniles of the same age. For adults, however, under scenarios in which tolerance is implemented, the probability of mortality is the sum of the base level of mortality and an additive value scaled by tolerance. For instance, if the additional mortality is a maximum of 2%, a completely tolerant eagle will have a 2%
greater probability of mortality than a completely non-tolerant individual. The mortality rates for individuals between these two extremes are linear. The increased mortality cost of tolerance seemed likely given that eagles continue to suffer from persecution (Russell and Franson 2014). Breeding age eagles reset many state variables (whether they are incubating, provisioning food to nestlings, if they successfully fledged young in the current year, color) during this interbreeding season period. The model assumes strong nest site fidelity by adult eagles, so paired eagles remain on a current nest over subsequent years, unless their mate dies, or the breeding-season OHV level exceeds their tolerance. The occupancy probability of nests is also determined during the interbreeding season. If the tolerance levels of either eagle on a nest precludes them from occupying that nest, both eagles in that pair will leave that nest and attempt to pair (potentially with different mates) and establish elsewhere.

In each timestep of the breeding season, eagles increase their age by one day and the daily OHV volume is calculated at each nest. Each nest also records whether it is occupied by a pair of eagles and eagles check to ensure the nest they are moving towards has not become occupied. Unpaired eagles attempt to pair, with males selecting empty nests and females selecting unpaired males with nests. The probability of a particular nest becoming occupied is influenced by the breeding-season OHV level of the territory. Eagles move towards their chosen nest, if they are not already there, and if multiple pairs of eagles chose the same nest, the pair that arrives first will occupy the nest. Once a pair is at a nest, the nest is deemed occupied and no other eagles occupy it. Eagles move through an initialization period where they assort themselves with a single mate, and establish on a nest. If no nests are available eagles become floaters and move randomly until a nest or mate becomes available.

Once eagles are paired, the likelihood of egg-laying is influenced by the early-season pedestrian activity in the territory. If pairs lay eggs, each female can lay one or two eggs (representing what will become 1 or 2 nestlings). Eggs are incubated by the female for 45 days. The model does not account for within clutch infertility or individual egg mortality, between laying and hatching, as no reliable data exists for these factors. Eagle offspring may be of either sex and the tolerance of offspring to human disturbance can be randomly determined, inherited from the mother or imprinted based upon the natal nest characteristics. Eggs that reach 45 days old turn into nestlings, and remain so for 63 days. During both these stages, entire clutches and broods are subject to nest survival probabilities based on short-term OHV use. When nestlings reach 63 days, they fledge into juveniles, their mother’s “Success?” status turns to true and, if habituation is enabled in TRAILS, the tolerance of the adult pair can increase. Juveniles remain out of the breeding population for 4 years, and are stationary in the model. Juveniles experience differential rates of mortality in their first few years (Table 2), but if they reach breeding age (5 years), they can select a nest and a mate, the same as any adult eagle would.

Each year, at the end of the potential egg-laying period, TRAILS tracks the number of available territories, the number of occupied territories and the number of egg-laying pairs. It also records the mean tolerance of all territorial eagles. At the end of the breeding season, the model reports the number of nests that fledged young. TRAILS stops running after 100 years have elapsed or when no eagles remain in the population.

Design Concepts

Basic Principles- In TRAILS, the probability that young fledge from a nest is based on the compound probabilities of a nest being occupied, a pair laying eggs, and a nestling surviving the incubation and brood-rearing stages. In this model it is assumed that these probabilities are affected by recreational activity at nests. Furthermore, this model is built on the concepts of tolerance whereby different individuals are more or less sensitive to human disturbance, the tolerance of individuals can change over time and that experiences as nestlings can influence the tolerance of an individual (Davis and Stamps 2004, Bejder et al. 2009).

Emergence- Several population-level properties emerge from the interaction of eagles with each other and their environment. Most basically, the population growth rate is an emergent property. In addition, the population size and territory occupancy at the end of the simulation and the time to population extinction emerge. Also, the average tolerance of the population emerges from model behavior. Other patterns that emerge include: the average age at death of eagles, the mean number of young produced by the population per year, the mean number of young per pair, the mean number of eggs per pair, the mean success rate of eagle pairs and the mean proportion of successful territories.
Adaptation- Eagles in the model exhibit little true adaptation. Individuals only select nests with disturbance levels below their tolerance, thus preferentially choosing nests with low human disturbance relative to their tolerance level.

Objectives- The goal of breeding-age eagles is to find a mate and suitable nest and to fledge offspring at that nest. Therefore, eagles will avoid nests with relatively high human disturbance.

Learning- In most cases, simulated eagles do not explicitly learn. However, when habituation is simulated, eagles may increase their tolerance to human disturbance if they successfully fledge offspring in a disturbed area, thus learning from previous experience.

Sensing- Eagles are able to sense nearly everything about themselves and their environment but not about other eagles. Individuals know their own state variables (e.g., sex, location, pairing status, tolerance, etc.). Eagles can sense all potential nests and assess whether they are currently occupied by an eagle pair. In addition, eagles can sense the occupancy probability of unoccupied nests.

Interaction- Interaction among individuals is essentially between mates and competition between pairs for nests. Male and female eagles must find a suitable nest and a mate. If either is unavailable, simulated eagles become floaters. In addition, if two eagle pairs choose the same nest, the first to arrive will occupy that nest and the other pair must find another nest.

Stochasticity- Stochasticity is employed throughout much of TRAILS. The likelihood of egg laying, nest survival, juvenile survival and adult survival are all described via probabilities. Therefore, the execution of these processes depends on random number draws compared to those calculated probabilities. The coefficients in the probability calculations themselves, along with the amount of recreational volume are determined stochastically by drawing coefficient values from a normal distribution defined by a mean and standard error. Finally, the number of eggs laid (resulting in either 1 or 2 nestlings; a simplification per Steenhof et al., 1997) and the sex of the offspring is determined stochastically with equal probability.

Observation- Many aspects of the model are observed, without error or sampling bias, during model runs. The number, success rate, age and tolerance of eagles are tracked during simulations. In addition, the occupancy and success of nests and recreational volumes influencing nests are also determined.

Initialization

At the beginning of the model, twenty five nests are created, and occur at the same locations every time, to represent real world locations of eagle territories. Each nest is initialized with a set suite of recreational pressure values – breeding-season OHV level, daily OHV volume, trail density, early-season pedestrian level – to correspond with known recreational activity at particular nests (Spaul 2015, Spaul and Heath in review). All nests begin the simulation unoccupied. The probability of occupancy for each nest is then calculated based on the breeding-season OHV level at that nest.

Forty four eagles, 22 males and 22 females, are established at the start of the simulation to approximate a plausible initial condition for golden eagles in southwestern Idaho (Spaul 2015, Spaul and Heath in review). All simulated eagles begin unmated and without a territory. Each eagle is randomly assigned a tolerance value between 0 and 1. A tolerance value of 1 represents a fully tolerant eagle with no perception of recreation. A tolerance value of 0, on the other hand, would be a fully sensitive (intolerant) eagle with maximal perception of recreation and its disturbing influence. In addition, the age of each initial eagle is set as a random age between 5 and 16 years. Simulated eagles start in a random location within the modeled landscape.

Input Data

This model does not use input data to represent time-varying processes
Submodels

Territory Occupancy Submodel

Using a suite of recreation variables, a generalized linear mixed model (GLMM) was developed to assess temporal variation in recreation levels across the entire breeding season, and its influence on territory occupancy was used to calculate the probability of occupancy for each nest (Spaul 2015, Spaul and Heath in review). The probability of nest occupancy was primarily driven by breeding-season OHV level following the equation:

\[
\text{logit}(P(\text{nest0occupancy})) = 4.5021(\pm 1.3418) - 1.6482(\pm 0.6797) \times \text{OHV}_\text{vol}
\]

Egg Laying Submodel

The likelihood of whether eagle pairs initiated breeding was predicted by the level of pedestrians before the mean laying date within our study population (Spaul 2015, Spaul and Heath in review) following:

\[
\text{logit}(P(\text{eggLaying})) = 0.6149(\pm 0.4702) - 1.5697(\pm 1.2946) \times \text{Ped}_{\text{PreLay}}
\]

Eagle pairs that successfully lay eggs lay a clutch of either one or two eggs (with even probability) and the likelihood of each egg being either male or female is equivalent.

Daily OHV Volume Submodel

Second order models additive effects of Julian Week and (Julian Week)^2 predicted OHV level, for both midweek and weekend days. The following models were used:

\[
\ln(Daily\_OHV\_VOL\_\text{weekend}) = -7.60473(\pm 0.57610) + 0.49903(\pm 0.03624) \times \text{Week} - 3.18046(\pm 0.22907) \times \text{Week}^2
\]

\[
\ln(Daily\_OHV\_VOL\_\text{midweek}) = -9.32380(\pm 0.82832) + 0.48584(\pm 0.05249) \times \text{Week} - 2.86007(\pm 0.31597) \times \text{Week}^2
\]

Daily OHV levels were then multiplied by territory modifiers (Rec_Generic) to create realistic differences in recreation volumes between nests.

Nest survival Submodel

Golden eagle nest survival is nesting stage specific (incubating or brood-rearing stage), and negatively influenced by the level of OHVs as it changed throughout the season (Int_OHV_Day). The equation used to model nest survival was:

\[
\text{logit}(P(\text{survival})) = 4.8025(\pm 0.3741) + 1.7838(\pm 0.8087) \times \text{Stage} - 0.5893(\pm 0.2183) \times \text{Int}_\text{OHV}_\text{Day}
\]

Where \text{Stage} is 1 for incubating eggs and 0 for brood-rearing. As these models were created using data from 8-10 day trail camera surveys, daily OHV levels were tabulated in running 9 day averages, and input into TRAILS as such. Because of the high variation in such recreation data, over 100 year time-scales, occasionally this created Daily nest survival probabilities below 0.925 for the incubation-stage and below 0.965 for the brood-rearing-stage, values at the limit of observed data. In such cases, survival probabilities were modified to match minimum daily nest survival probabilities at these levels. If a nest failed, all offspring in that nest died.
Annual Recreation Volume Increase Submodel

Changes in annual recreation parameters were calculated for the seasonal averages of recreation use and trail density, by following the simple equation:

\[
Daily_{OHV\_VOL} = Daily_{OHV\_VOL} \times (1 + Annual_{Rec\_Vol\_Change})^{(year-1)}
\]

Tolerance and Habitation Submodels

Tolerance by individuals was modeled simply, where tolerance was the inverse of sensitivity which was measured between 0 and 1. Individual eagles could not occupy a nest if the occupancy probability of that nest was less than the sensitivity of the eagle. Importantly, the tolerance of an eagle affects its perception of the recreation activity around it. For instance, an eagle with a sensitivity of 0.5 would only observe, and be affected by, half of the recreational pressure of that by an eagle with full sensitivity. For nestlings, sensitivity could be determined in one of 3 ways. Under both ‘random’ and ‘habitation’ scenarios, nestlings were given a sensitivity value drawn from a uniform distribution between 0 and 1. With ‘inheritance’ scenarios, nestlings inherited identical sensitivity levels as their mother. When ‘imprinting’ was turned on, imprinted eagles took as their sensitivity value the occupancy probability of their natal nest less a buffer value (to ensure they could occupy nests similar to their own natal nest). Finally, when ‘habitation’ was implemented, if eagles successfully fledged offspring at a nest within a user-controlled range of the eagle’s sensitivity, the eagle would decrease its sensitivity by the same user-controlled amount. For instance, if a male with sensitivity of 0.75 (and a user-set buffer value of 0.2) successfully fledged young at a nest of occupancy probability of 0.8, the eagle would then have a sensitivity value of 0.55 the following year.

Mortality

Mortality of post-fledging eagles occurs once per year. The annual mortality rate for juveniles age 1 was set to 16%, while for juveniles age 2-4 the probability of mortality was 21% each year. For adults, the baseline mortality rate was 2% (Table 2). However, under scenarios in which tolerance was implemented the probability of mortality is the sum of the base level of mortality and an additive value of 2% scaled by tolerance. Therefore, a completely tolerant eagle would have a 2% greater probability of mortality than a completely non-tolerant individual. The mortality rates for individuals between these two extremes were scaled linearly.

Data Evaluation

This TRACE element provides supporting information on: The quality and sources of numerical and qualitative data used to parameterize the model, both directly and inversely via calibration, and of the observed patterns that were used to design the overall model structure. This critical evaluation will allow model users to assess the scope and the uncertainty of the data and knowledge on which the model is based.

Summary

Most aspects of this model have been parameterized based upon empirically determined aspects of golden eagle nesting and disturbance. Many of these relationships were determined as part of field research coupled with this model. Others were drawn from published accounts of various aspects of golden eagle ecology.

Disturbance

The main processes of the model relate to recreational disturbance of nesting eagles. The parameterization of these processes in the model draw mainly from coupled research within the study area in southwestern Idaho (Spaul 2015). In that research, nests were located and at each nest the occupancy of nests was recorded, egg-laying at nests was determined and the success of fledging was assessed. In addition, the level of recreational activity (both motorized and non-motorized) was measured near nests. From these data, generalized linear mixed models were created to determine the effect of different recreation types on the various stages of golden eagle nesting. These equations (along with estimation error) were then used to parameterize the effect of disturbance on eagles. In
addition, simple quadratic equations for recreational activity (separately determined for motorized and non-
motorized recreationists for both weekdays and weekends) was used to model changes in recreational pressure
over time. These empirical models were created to assess, in the short term, the same aspects of golden eagle ecology
as the individual based model and both were applied to the same geographical region.

Mortality

Mortality of juvenile (fledged) and adult golden eagles was not the primary focus of this model. Nonetheless,
including mortality for post-fledged individuals was necessary for basic population dynamics. Mortality was
implemented as a yearly phenomenon with separate mortality rates for juveniles in year 1, juveniles in years 2–4
and adults (age > 4). The juvenile mortality rate in the first year was 16% and 21% in each of the following
three years. These values were based upon a study of a population of golden eagles in California (Hunt 2002) and
correspond closely to studies of juvenile golden eagle mortality in other regions (Whitfield et al. 2004, McIntyre et
al. 2006). Adult mortality, on the other hand, was set at a range of 2% - 4% annually (depending upon tolerance).
Studies of golden eagles often estimate adult mortality at higher rates with values ranging from 9% to 25% annually
(Harmata 2002, Hunt 2002). A lower valued was used in this model for three reasons. First, this model does not
include immigration of individuals into the population which would bolster the population size. Instead a
lower mortality rate was used to offset this excluded aspect. Second, many studies of golden eagles are conducted
upon migratory populations (e.g., Harmata 2002). Our study area, on the other hand, includes only a non-migratory
population (Spaul 2015). A population not subject to the stress of migration could be expected to have a lower
mortality rate than that of a migratory population. Finally, the adult mortality rate was calibrated to a 2% baseline
so that basic patterns of eagles in our study area (namely the slowly declining but extant population; Steenhof et al.
1997) could be properly matched. Finally, any eagle that exceeds 20 years of age dies in order to prevent
unreasonably old eagles from occurring in the population (Kochert et al. 2002).

Tolerance

Tolerance, habituation and habitat imprinting in the model were drawn from a theoretical rather than empirical
understanding. Little research has been conducted on tolerance and habituation in golden eagles. Thus, quantifying
such behaviors accurately was not possible. Instead, simple rules for each were implemented so that the
potential effect of each could be explored.

Other Eagle Biology

Other aspects of basic golden eagle biology used in the model have been drawn from various published sources.
The number of potential fledglings was set at either 1 or 2 (with equal probability) to correspond with observed brood
sizes at fledging in southwestern Idaho (Steenhof et al. 1997). The length of the breeding season (190 days) and
incubation period (45 days) and the age of eagle fledging (after 63 days) and sexual maturity (4 years) were also
derived from demographic studies of golden eagles, most of which were conducted in Idaho (Steenhof et al. 1983,

Conceptual Model Evaluation

This TRACE element provides supporting information on: The simplifying assumptions underlying a model’s
design, both with regard to empirical knowledge and general, basic principles. This critical evaluation allows model
users to understand that model design was not ad hoc but based on carefully scrutinized considerations.

Summary

A flow diagram of the conceptual model is represented in Figure A1. Details regarding model design and conceptual
framework are presented in the model description and data evaluation sections. While the assumptions of the empirical
research underlying this model are not addressed here, the general framework for this model is discussed below.
The basis of this model is the nest survival model whereby the likelihood of a successful nest is determined in stages representing nest occupancy, egg laying and offspring survival. Such models assume that nest success in all stages can be quantified based upon external factors that drive behavior. In this model it is assumed that recreational disturbance is the driving factor in determining whether a nest is occupied, whether eggs are laid and whether the offspring survive (Steenhof et al. 2014, Spaul 2015). Other factors associated with nesting success are treated as stochastic noise. Other aspects of eagle behavior were simplified including nest and mate selection and the competition among individuals for territories. Finally, the role of tolerance and habituation was constructed in a theoretical, rather than empirical, fashion due to the paucity of quantitative data on tolerance and habituation of golden eagles.

### Implementation Verification

*This TRACE element provides supporting information on:* (1) whether the computer code implementing the model has been thoroughly tested for programming errors, (2) whether the implemented model performs as indicated by the model description, and (3) how the software has been designed and documented to provide necessary usability tools (interfaces, automation of experiments, etc.) and to facilitate future installation, modification, and maintenance.

### Summary

To verify proper implementation of the code a number of tests in various forms were conducted. At the most basic level, the code was checked for syntax errors during production. In addition, focused tests of individual submodels were performed and the results observed both visually and through the use of various forms of output. In addition, spot checks of the attributes of individual agents were compared to those calculated manually and extreme scenarios were undertaken to function as a ‘stress test.’ Finally, the entire code was reviewed independently by researchers not associated with code development.

Tests of model execution varied in their complexity and focus but all were executed to ensure that the entire model was implemented properly.

- Throughout code development, the syntax was verified via the syntax checker in NetLogo to ensure that each line of code followed proper structuring.
- Visual testing was used extensively throughout model development to ensure proper functioning. For instance, parameters were simplified to isolate only pairing of eagles. Because of the color coding and unique sizing of individuals, the improper association of birds (e.g., >2 per pair, incorrect sex distribution, individuals not assessing pairing correctly, etc.) could be readily tested.
- The use of both immediate and summary output was employed throughout nearly every submodel. Most commonly, tracking of internal variables and processes were done by simply writing out the values of variables (via show commands in NetLogo). In addition, summary output at the conclusion of simulations was also used to ensure that derived variables (e.g., slope of regression lines) were properly determined.
- Similarly, extensive spot checking of agents and nests was conducted. This allowed for the examination of variables midstream and enabled us to compare the changes in particular variables to those calculated manually to ensure that they aligned properly.
- This model was also tested using extreme scenarios (e.g., values set to 0) and any associated errors such as divisions by 0 were corrected. These simulations also allowed us to determine that model output was emergent within realistic constraints rather than imposed across all possible simulation setups.
- Finally, the full model code was reviewed by an independent researcher unassociated with code development (but familiar with the model purpose and the NetLogo language)
This model was constructed in NetLogo 5.1.0 (Wilensky 1999), a free software platform. The model can be run using NetLogo on all major operating systems. This model can be explored using the switches and sliders on the graphical user interface. In addition, more systematic exploration of the model’s parameter space and associated output can be conducted using the ‘behavior space’ capabilities of NetLogo.

**Model Output Verification**

This TRACE element provides supporting information on: (1) how well model output matches observations and (2) how much calibration and effects of environmental drivers were involved in obtaining good fits of model output and data.

**Summary**

The implementation of this model only involved the calibration of a single parameter (adult annual mortality). Once completed, pattern matching and model performance were satisfactory. Measures of how well model output matched empirical observations are presented in the model output corroboration section of this document.

Only the adult annual mortality rate deviated from published estimates. Published estimates from the closest system (both geographically and biologically) were 9%. However, when this value was used with other parameterization, the population quickly went extinct. Instead, when values of 2% - 4% were used, the population remain extant (though with some declines) as expected based upon empirical data (Steenhof et al. 1997). We believe this calibration was warranted and appropriate for two reasons. First, this model does not include immigration of individuals into the population which would bolster the population size. Instead a lower mortality rate was used to offset this excluded aspect. Second, many studies of golden eagles are conducted upon migratory populations (e.g., Harmata 2002). Our study area, on the other hand, includes only a non-migratory population (Spaul 2015). A population not subject to the stress of migration could be expected to have a lower mortality rate than that of a migratory population.

**Model Analysis**

This TRACE element provides supporting information on: (1) how sensitive model output is to changes in model parameters (sensitivity analysis), and (2) how well the emergence of model output has been understood.

**Summary**

We examined the sensitivity of the model to changes in a number of the model parameters. We examined the effect of systematic variation of each parameter on all of the output from the model used in this context. Emergence of model output is explored more thoroughly in the model output corroboration section and main manuscript.

Many of the equations used to construct most of this model have been drawn from empirically derived, published studies. In addition, we have included the variance associated with published estimates in our model so that errors associated with those studies have been incorporated into this model. Therefore, we only conducted sensitivity analysis on the parameters in this model that were not based upon our own coupled research. Thus, we systematically varied the annual adult mortality rate, the habituation effect, imprinting (habitat) effect, juvenile mortality for each of years 1-4, and the tolerance effect on additional mortality. For each parameter we conducted 100 simulations where all other parameters were held constant but the parameter of interest was varied from -50% to +50% from baseline in increments of 10%. This resulted in a total of 8800 simulation runs (100 replicates * 11 possible parameter values * 8 parameters varied). The results of these simulations were then analyzed using the ‘spartan’ package (Alden et al. 2013, 2014) in program R (version 3.1.1; R Core Team 2012). For all response variables, a Vargha-Delaney A-Test (with the standard significance level of 0.21) was conducted when varying each parameter. All model output was relatively insensitive to both annual adult mortality and the level of additive cost of tolerance (Figures A2 and A9). Similarly, model output not related to population sensitivity/tolerance was insensitive to the level of tolerance change from a habituation event and the leeway given to tolerance of eagles.
with habitat imprinting. The model was somewhat sensitive, however, to the juvenile mortality parameters (Figures A3 and A4). In particular, population growth and nest occupancy was most strongly affected by perturbations to these parameters (Figures A5-A8).

Model Output Corroboration

This TRACE element provides supporting information on: How model predictions compare to independent data and patterns that were not used, and preferably not even known, while the model was developed, parameterized, and verified. By documenting model output corroboration, model users learn about evidence which, in addition to model output verification, indicates that the model is structurally realistic so that its predictions can be trusted to some degree.

Summary

A number of patterns from data independent of model construction have been used to evaluate the ability of the model to realistically represent golden eagle population dynamics.

This model capitalizes upon much of the empirical research that has been conducted on golden eagles in Idaho. However, a number of patterns of golden population dynamics were not directly built into the model framework but, instead, emerged due to the interaction of other factors in the model. Below we compare the output from the model with and without recreational disturbance to those anecdotal or empirical data. Results without recreation were assessed since this may better represent patterns from past conditions (e.g., 20 years ago) than the model with recreation. [Other scenarios have been more fully explored in the main manuscript].

Population Stability

Populations of golden eagles in Idaho have been stable or slowly declining over the past few decades but, importantly, have not shown dramatic population declines or extinction (Steenhof et al. 1997). Our model predicted that without recreational disturbance, eagle populations would have population growth and a robust population size (Figure A10). Under current recreational pressure, eagle populations would be expected to remain relatively static or exhibit slow population declines (Figure A10). These patterns matched expectations on both accounts.

Reproduction

Production of young in the model was an emergent property resultant from a number of interacting features such as nest success, sex ratio, nest discovery and recreational pressure. Simulated numbers of mean young produced by the population and both the number of mean eggs and the mean number of young produced per eagle pair occurred within the confidence interval of values measured in the same area (Figure A10; Steenhof et al. 1997). Similarly, the proportion of successful eagle pairs and the proportion of successful territories were relatively similar to those measured previously (Figure A10; Steenhof et al. 1997). This is particularly true for simulations that omitted recreational disturbance. Such a scenario may be more realistic than when disturbance was included as recreational use of eagle habitat was less pronounced when that research from which the pattern was derived was conducted and the effects of disturbance on nesting eagles may have taken effect primarily within the past 10 – 20 years (Steenhof et al. 2014).

Nest Occupancy

The proportion of nests occupied under scenarios without recreational disturbance closely matched those measured in field studies (Figure A10; Steenhof et al. 1997). With disturbance implemented, however, nest occupancy was lower than those of empirical research. This could be due to the long period of disturbance effect in simulations (100 years) or the fact that the field occupancy measurements were taken when recreational disturbance was less than that of current levels (Steenhof et al. 2014).


Figure A1. Flow diagram of individual based model of recreational disturbance of nesting golden eagles.
Figure A2. Sensitivity analysis of the mortality of adult eagles. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A3. Sensitivity analysis of the degree of behavioral change following habituation of eagles. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A4. Sensitivity analysis of the flexibility in nests available to eagles with habitat imprinting. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A5. Sensitivity analysis of the mortality of juvenile eagles in their first year. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A6. Sensitivity analysis of the mortality of juvenile eagles in their second year. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A7. Sensitivity analysis of the mortality of juvenile eagles in their third year. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A8. Sensitivity analysis of the mortality of juvenile eagles in their fourth year. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A9. Sensitivity analysis of the mortality cost of eagle tolerance. Value range from -50% of baseline to +50% of baseline in 10% increments. A-score values greater than 0.71 or less than 0.29 are considered large differences and suggest potentially sensitive parameters.
Figure A10. Pattern matching of model output to field measurements of golden eagles. Panels 1-2 display population stability (solid line). Panels 3-8 display the mean (solid line) and 95% confidence interval (dashed line) for measurements of Steenhof et al. (1997)
Figure B1. Mean annual population growth for simulated eagle populations under recreation pressure ranging from current levels (0 annual change in recreation) to a 3% annual increase (0.03 annual change in recreation). Panels reflect varying ways in which eagles develop tolerance: without any tolerance (No tolerance), randomly assigned (Random), genetically transferred (Inherit), habitat imprinting (Imprint) or through habituation (Habituate).
Figure B2. Time until local extinction for simulated eagle populations under recreation pressure ranging from current levels (0 annual change in recreation) to a 3% annual increase (0.03 annual change in recreation) [Note: 100 years reflects no extinction]. Panels reflect varying ways in which eagles develop tolerance: without any tolerance (No tolerance), randomly assigned (Random), genetically transferred (Inherit), habitat imprinting (Imprint) or through habituation (Habituate).
Figure B3. Final population size (after 100 years) for simulated eagle populations under recreation pressure ranging from current levels (0 annual change in recreation) to a 3% annual increase (0.03 annual change in recreation). Panels reflect varying ways in which eagles develop tolerance: without any tolerance (No tolerance), randomly assigned (Random), genetically transferred (Inherit), habitat imprinting (Imprint) or through habituation (Habituate).
Figure B4. Final nest occupancy (after 100 years) for simulated eagle populations under recreation pressure ranging from current levels (0 annual change in recreation) to a 3% annual increase (0.03 annual change in recreation). Panels reflect varying ways in which eagles develop tolerance: without any tolerance (No tolerance), randomly assigned (Random), genetically transferred (Inherit), habitat imprinting (Imprint) or through habituation (Habituate).
Figure B5. Final mean population sensitivity value (after 100 years) for simulated eagle populations under recreation pressure ranging from current levels (0 annual change in recreation) to a 3% annual increase (0.03 annual change in recreation). Panels reflect varying ways in which eagles develop tolerance: without any tolerance (No tolerance), randomly assigned (Random), genetically transferred (Inherit), habitat imprinting (Imprint) or through habituation (Habituate).