

BIRD TOLERANCE TO HUMAN INTRUSION IN WYOMING MONTANE FORESTS¹

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Abstract. Human intrusion can be a serious problem for birds because it can cause displacement, prevent access to resources, and reduce reproduction and survival. The factors that influence avian tolerance to intrusion are poorly understood. We studied passerine responses to intrusion in Wyoming montane forests during the breeding season by using two indices of intrusion tolerance: detectability period, the amount of time that a bird remains near its initial flush point; and approach distance, how close one can get to a bird before it flushes. A solitary observer experimentally approached focal individuals and recorded detectability period, approach distance, the seasonal and daily timing of intrusion, number of nearby conspecifics, number of nearby heterospecific individuals, and surrounding vegetation conditions. Using data from the literature, we also assessed influences of migratory status, body mass, conspicuousness, and height above the ground at which species are active during the breeding season. Detectability period was significantly shorter, indicating intrusion tolerance was lower, when fewer conspecifics were nearby. Approach distance was significantly longer, indicating tolerance was lower, for more-conspicuous species and for species that are active closer to the ground. Effects of other variables studied were not significant. These results demonstrate that social and biological factors can influence tolerance to intrusion. Intrusion-induced behaviors such as nest abandonment and decreased nest attentiveness have led to reduced reproduction and survival in species that are intolerant of intrusion. With knowledge of factors that influence tolerance, the risk of disturbing birds that are sensitive to intrusion could be reduced.

Key words: bird disturbance, human intrusion, intrusion tolerance, montane forest, Wyoming.

INTRODUCTION

Human intrusion is environmental disturbance that involves the mere presence of people. It can influence avian fitness by inducing abnormal vigilance, preventing access to important resources, and reducing fecundity and survival (Boyle and Samson 1985, Rodgers and Smith 1995, Hill et al. 1997). In many wildlands, such effects stem from intrusions by ecotourists and recreationists (Purdy et al. 1987, HaySmith and Hunt 1995, Knight and Gutzwiller 1995). Avian tolerance to

intrusion varies considerably among and within species (Erwin 1989, Burger and Gochfeld 1991, Knight and Temple 1995a), and differences often are highly context-specific (Wilson et al. 1991, Knight and Cole 1995, Hill et al. 1997). Such variability has made it difficult to determine which species may be sensitive to intrusion. In turn, the lack of knowledge about which species are likely to be intolerant of intrusion complicates efforts to minimize impacts on birds and simultaneously permit human use of natural landscapes (Knight and Temple 1995b). Knowledge of factors that influence avian tolerance to intrusion could be used to reduce the risk of disturbing birds that are sensitive to intrusion.

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Avian tolerance to intrusion can depend upon intrusion timing during the breeding season, as some species that are disturbed early in the nesting cycle will abandon their nests (Knight and Cole 1995). Birds that replenish energy stores used during the night by feeding early the next day may be less tolerant to morning intrusions than to intrusions occurring later (Gutzwiller and Marcum 1997). Birds usually exhibit less tolerance to a human intruder as avian group size increases (Knight and Cole 1995), and when vegetation blocks visual contact between birds and human intruders, birds seem more tolerant to intrusion (Knight and Temple 1995b). In response to approaching humans, migrant species seem to be less tolerant than residents (Burger and Gochfeld 1991), and larger species appear to be less tolerant than smaller species (Cooke 1980, Humphrey et al. 1987, Knight and Cole 1995). Some conspicuous bird species, because they are more noticeable than inconspicuous species, may instinctively be more evasive toward potential predators (Baker and Parker 1979, Götmark and Unger 1994). This suggests that conspicuous species would be less tolerant than inconspicuous species to an approaching human. Because of their greater vulnerability to walking predators, species that are active on the ground or in the understory might be less tolerant to human intrusion than overstory species (Burger and Gochfeld 1991, Holmes et al. 1993).

Detectability period, the amount of time that a bird remains visible near its initial flush point, has been used as a measure of intrusion tolerance, with shorter detectability periods reflecting less tolerance (Gutzwiller and Marcum 1997). Approach distance, how close one can get to a bird before it flushes, also has been used as a tolerance index, with longer approach distances indicating less tolerance (Humphrey et al. 1987, Erwin 1989, Burger and Gochfeld 1991). Using detectability period and approach distance as indices of intrusion tolerance, we studied responses to human intruders by five bird species that are encountered frequently by recreationists in Wyoming montane forests during the breeding season: Gray Jay (*Perisoreus canadensis*), Mountain Chickadee (*Parus gambeli*), American Robin (*Turdus migratorius*), Yellow-rumped Warbler (*Dendroica coronata*), and Dark-eyed Junco (*Junco hyemalis*). Our objective was to assess whether intrusion tolerance was associ-

ated significantly with the seasonal and daily timing of intrusion, number of nearby conspecifics, number of nearby heterospecific individuals, vegetation density, migratory status, body size, conspicuousness, and the vertical height above the ground at which species are active.

METHODS

STUDY AREAS

Data were collected at sites between 2,500 and 3,045 m elevation in two parts of the Medicine Bow National Forest: the Snowy Mountains, approximately 70 km WNW of Laramie, Wyoming (41°32'N, 106°20'W), and Pole Mountain, about 16 km SE of Laramie, Wyoming (41°15'N, 105°23'W). Vegetation conditions included riparian areas, meadows, clearcuts, groves of aspen (*Populus tremuloides*), stands of lodgepole pine (*Pinus contorta*), and mixed-conifer stands containing limber pine (*Pinus flexilis*), Engelmann spruce (*Picea engelmannii*), and subalpine fir (*Abies lasiocarpa*). Common shrub species, precipitation data, and minimum and maximum temperatures for the study areas are presented in Gutzwiller et al. (1997).

DATA COLLECTION

During 1989–1993, we randomly selected a total of 93 1.6 x 1.6 km forested sections in both study areas and randomized the order in which sections were visited. Each section was visited only once during the entire 5-year study. From late May to early August each year, data were collected between 07:00 and 16:30 Mountain Standard Time, the daily period during the breeding season when birds were most likely to be disturbed by recreationists in our study region. Within a given section, before detecting any individuals, a solitary observer walked to the forest vegetation that was closest to the point of vehicle access and that was at least 100 m from the nearest used road, campground, or recently logged area. From this vegetation, the observer used a forest map to choose an initial direction to walk that would maximize the amount of forest vegetation that could be covered with parallel travel lines spaced at least 300 m apart. This sampling scheme enabled the observer to maximize the number of individuals that could be encountered in each section.

The observer walked approximately 1,600 m along each travel line. Repeated trials with the same individual bird, and hence potential prob-

lems with lack of independence among observations, were unlikely because consecutive encounters occurred far enough apart (≥ 300 m) that different territories were encountered, the same species was never approached twice in a row, 25 min or more elapsed between encounters with the same species, and the observer moved farther and faster through habitats than did individual birds, which typically moved only meters to tens of meters as they maintained territories, tended nests, fed, and rested.

We studied species that are encountered by wildland recreationists in our study region, but in both study areas the specific encounter sites at which we gathered data were hundreds of meters to several kilometers from probable and known sites of intrusion by recreationists, resource managers, and other people. No one except the observer was present at encounter sites during data collection. Thus, during the study season, the individuals we studied probably experienced little if any intrusion prior to our trials. Except for consecutive individuals of the same species, an observer experimented with individuals as they were encountered. Only individuals that an observer knew were initially perched or standing and that flushed in response to the observer's approach, as indicated by their pre-flush behavior and subsequent direction of flight, were involved in the present analysis. Data were not collected when windspeed was > 20 km hr⁻¹, as measured with a hand-held anemometer, or when there was heavy rain, but data were gathered during all other weather conditions and in the various forest types that recreationists might encounter in the study areas.

Between encounters, the observer walked at a pace of about 3–5 km hr⁻¹ along the original parallel lines of travel. When a bird was observed, the observer temporarily left the line of travel and approached the bird directly and steadily at this same walking pace. When it flushed, the observer stopped and timed with a stopwatch to the nearest sec how long the bird remained visible within 10 m of its initial flush point; this amount of time was the detectability period. When it flew beyond this distance, the trial ended. Before data collection began, the observer practiced estimating the 10-m distance and checked his or her estimates with a meter tape; with practice, observers routinely estimated the distance to within about 1 m. For each focal individual, approach distance was mea-

sured with a meter tape to the nearest meter. Approach distance was the distance between the observation point, which was the place where the observer stopped when the bird flushed, and the flush point, which was the ground position from which the bird flushed or a vertical projection to the ground from an elevated flush point. When a group of birds was encountered, the first individual seen was the focal individual.

Immediately after each encounter, the date in terms of the number of days since the fieldwork began each year, time of day to the nearest min, study area (Snowy Mountains, Pole Mountain), and bird species were recorded. Also noted were the number of conspecifics and the number of heterospecific individuals within 25 m of the focal individual. These latter two variables were recorded for the interval between the beginning of the observer's approach toward an individual and the point in time when that particular encounter ended. Observers practiced estimating the 25-m distance before data collection began and were regularly able to estimate the distance to within about 2 m.

To determine possible habitat influences on species' responses, visibility measurements were completed at the observation point and at the flush point. To obtain visibility estimates, the observer measured in four directions, with a meter tape to the nearest meter, the distance between himself or herself and the nearest edge of the nearest vegetation that obstructed his or her view at eye level, which was about 1.6 m. The first direction was along a randomly selected bearing chosen with a random numbers table, and the three remaining measurements were made along bearings that were 90°, 180°, and 270° from the initial random bearing. We calculated the mean and coefficient of variation (CV) for the four visibility distances for the observation point; the same calculations were made for the four distances measured at the flush point. These measurements served as indices of vegetation density and its variability, and they enabled us to study the effects of habitat conditions immediately surrounding the observer and the focal individual.

Different observers collected data each year, but all observers used the same measurement techniques. Nevertheless, differences among observers or annual differences in environmental conditions and avian responses to intrusion may have induced yearly variation in the measure-

ments. We therefore recorded the year in which each observation was made. Migratory status (resident, migrant) was recorded for each species. A species was designated a migrant if it migrates more than 300 km and no individuals of that species are present in our study area year-round (Peterson 1990); otherwise a species was considered a resident, which included altitudinal migrants (Riffell et al. 1996). Body mass was used as an index of body size and was obtained from Dunning (1984). When separate mean mass values for males and females were provided for a given species, we used the average of the two means, otherwise the single mean mass value listed in Dunning (1984) was used. To estimate avian conspicuousness, we used the methods of Baker and Parker (1979), which rate species with brighter colors and greater color contrast within and among body regions as more conspicuous; higher numerical scores are indicative of greater conspicuousness. We used photographs and descriptions of species for the breeding season (Farrand 1983a, 1983b) to assess conspicuousness. Birds often feed and seek shelter in the vertical strata in which they nest (Dunlavy 1935, MacArthur 1958), and much time is spent at and near the vertical height of the nest during nest construction, egg laying, incubation, and the feeding and brooding of young. We therefore used the midpoint of the published range of a species' nest height (Terres 1980) as an index to the vertical height above the ground at which that species would be active during the breeding season; this height is referred to as "activity height" hereafter.

STATISTICAL ANALYSES

To assess separately whether each dependent variable (detectability period, approach distance) was associated with explanatory variables we measured in the field and obtained from the literature, we used a general linear model (PROC GLM, SAS Institute 1989) to conduct analysis of covariance. Categorical variables included year, study area, and migratory status. The remaining variables were entered as continuous variables. Study area and year were not of central interest in the present study, but we included them in analyses to control for any variation in bird responses that might be associated with them. Controlling for these extraneous effects enabled us to discern more clearly the effects on bird responses from environmental conditions

and species' biological traits, the foci of our analyses.

We applied a \log_{10} transformation to detectability period and approach distance. Histograms, normal-probability plots, and residual plots indicated that each model met statistical assumptions concerning linearity, error-term variance, and error-term normality (Ott 1993). Durbin-Watson statistics confirmed that there was no serial correlation and that observations for individual birds were independent (Ott 1993). For each dependent variable, we reported the influence of each explanatory variable based upon Type III sums of squares, which enable one to assess the influence of a given explanatory variable after the effects of all other such variables in a general linear model analysis have been accounted for (SAS Institute 1989). The signs of t statistics provided by PROC GLM were used to determine the directions of relations between dependent variables and continuous explanatory variables.

To improve statistical power, we used an a priori $\alpha = 0.10$ for all analyses (Nichols et al. 1984, Westmoreland and Best 1985). Compared to $\alpha = 0.05$, using $\alpha = 0.10$ reduced the probability of committing a Type II error but, without further control, would have increased the probability of committing a Type I error. Type I errors for simultaneous inferences were controlled with the following approach. For detectability period and approach distance separately, we considered the set of statistical tests for the 14 explanatory variables to be a distinct "family" (Miller 1981) of simultaneous tests because all 14 tests pertained to the same dependent variable and hence were related to one another. To assess the statistical significance of tests in each family, and to minimize Type I errors, we adjusted the α for individual tests using the sequential Bonferroni technique, which provides higher statistical power than the standard Bonferroni method when more than one of a group of tests is significant (Holm 1979, Rice 1989).

Our results for general linear model analyses are based upon dependent variables that were \log_{10} transformed, but the summary statistics we provide for dependent and explanatory variables are for observed (untransformed) data.

We considered whether vegetation conditions may have influenced the probability of detecting nearby conspecifics and heterospecifics. For conspecifics and heterospecifics separately, we

TABLE 1. Biological traits of five bird species studied during the breeding season in Wyoming montane forests.

Species	Conspicuousness	Activity height (m)	Body mass (g)	Migratory status
Gray Jay	17.0	2.1	71.1	Resident
Mountain Chickadee	10.0	3.2	10.8	Resident
American Robin	22.5	3.8	77.3	Resident
Yellow-rumped Warbler	29.0	8.1	12.1	Migrant
Dark-eyed Junco	9.0	0.0	19.6	Resident

tested for such relations by using logistic regression (PROC LOGISTIC, SAS Institute 1989) to relate the presence or absence of conspecifics or heterospecifics to the visibility measures. We controlled for factors that might obscure effects of visibility variables by including in each model the following variables: study area, year, date, time of day, approach distance, detectability period, and species. For each of the two models separately, statistical significance of a variable was determined according to the sequential Bonferroni method described above; we used an a priori $\alpha = 0.10$ for each model. All assumptions of logistic regression (Hosmer and Lemeshow 1989, SAS Institute 1989) were met for each model.

RESULTS

SPECIES' TRAITS AND ENVIRONMENTAL CONDITIONS

We collected data for a total of 442 individual birds during the 5-year study. Sample sizes for levels of categorical variables were as follows: year: 89 (1989), 54 (1990), 80 (1991), 114 (1992), 105 (1993), study area: 291 (Snowy Mountains), 151 (Pole Mountain), migratory status: 385 (resident), 57 (migrant). Biological traits (Table 1) and summary statistics for temporal, social, and vegetation (visibility) variables (Table 2) describe the species and environmental conditions we studied.

DETECTION OF CONSPECIFICS AND HETEROSPECIFICS

The four visibility variables and other covariates studied with logistic regression were not significantly associated with the probability of detecting nearby conspecifics or nearby heterospecifics. These results suggest that vegetation conditions did not influence the observers' ability to detect conspecifics or heterospecifics.

DETECTABILITY PERIOD AND APPROACH DISTANCE

Descriptive statistics for detectability period and approach distance are listed by species in Table 3. For each general linear model: $n = 442$; $df = 4$ and 424 for year; and $df = 1$ and 424 for each of the other explanatory variables. The overall relation between detectability period and explanatory variables was significant ($F_{17, 424} = 7.6$, $P < 0.001$), but year and number of nearby conspecifics were the only individual variables that had significant effects (Table 4). The significance of the overall relation, and the individual relations involving year and number of nearby conspecifics, did not change for a reduced model in which all nonsignificant variables were deleted from the original model. Based upon the t -statistic sign, which did not change between original and reduced models, detectability period was positively associated with number of nearby conspecifics. Birds thus left the area near their

TABLE 2. Summary statistics for temporal, social, and vegetation variables during intrusion trials.

Variable	Mean \pm SD	Range
Number of days since late May	39.6 \pm 21.9	0-75
Time of day (hr)	11:14 \pm 2.4	07:14-16:14
Number of nearby conspecifics	0.6 \pm 0.8	0-5
Number of nearby heterospecific individuals	0.2 \pm 0.7	0-7
Mean visibility at observation point (m)	7.0 \pm 7.2	0.5-91.5
CV of visibility at observation point	0.7 \pm 0.3	0.0-1.8
Mean visibility at flush point (m)	6.3 \pm 6.6	0.3-79.0
CV of visibility at flush point	0.8 \pm 0.4	0.1-2.0

TABLE 3. Summary statistics for detectability period and approach distance during the breeding season for five bird species in Wyoming montane forests.

Species	n	Mean \pm SD (Range)	
		Detectability period (sec)	Approach distance (m)
Gray Jay	35	28.2 \pm 42.7 (1–170)	8.9 \pm 8.1 (1–39)
Mountain Chickadee	77	29.2 \pm 60.8 (1–399)	4.4 \pm 3.0 (1–13)
American Robin	112	17.8 \pm 58.6 (1–420)	12.1 \pm 6.8 (2–37)
Yellow-rumped Warbler	57	9.6 \pm 18.8 (1–86)	9.1 \pm 5.5 (2–27)
Dark-eyed Junco	161	32.9 \pm 122.4 (1–1,346)	7.5 \pm 4.1 (1–20)

initial flush point sooner, indicating they were less tolerant of the intruder, when fewer conspecifics were present within 25 m of them. This relation was significant after variation in detectability period associated with all other variables was accounted for.

The overall relation between approach distance and explanatory variables was significant ($F_{17, 424} = 18.4, P < 0.001$), but year, conspicuousness, and activity height were the only individual variables that were significantly influential (Table 4). The significance of the overall relation and the three individual relations did not change for a reduced model in which all nonsignificant variables were deleted from the original model. Based upon *t*-statistic signs, which also did not differ between original and reduced models, approach distance was positively associated with conspicuousness and negatively associated with activity height. Thus, approach distance was longer, indicating tolerance for intrusion was lower, for more conspicuous species and for species that are active closer to the ground during the breeding season. Each of

these relations was significant after variation in approach distance associated with all other variables was controlled for.

DISCUSSION

The lack of a study-area effect indicates that birds responded to intrusion similarly in both areas. Year effects may have occurred because we used different observers each year, but this possibility seems improbable because all observers were trained to use the same methods. An alternative hypothesis is that each year we encountered new individuals that had experienced a different collective mix of outcomes (positive, negative, neutral) in prior encounters with humans, and these experiences influenced birds' responses during our trials. Sustained changes in avian behavior induced by prior interaction with humans is common (Knight and Fitzner 1985, Knight and Temple 1986, Knight and Temple 1995a). Regardless of the actual cause, the extraneous effects of year were controlled for through our method of analysis and did not af-

TABLE 4. Results of general linear model analyses for detectability period and approach distance.

Explanatory variable	Detectability period		Approach distance	
	F	P	F	P
Study area	0.48	0.49	0.17	0.68
Year	15.37	<0.001	27.52	<0.001
Number of days since late May	0.36	0.55	0.10	0.75
Time of day	0.04	0.85	0.34	0.56
Number of nearby conspecifics	13.59	<0.001	0.00	0.95
Number of nearby heterospecific individuals	0.03	0.86	0.15	0.70
Mean visibility at observation point	0.04	0.84	2.27	0.13
CV of visibility at observation point	0.50	0.48	5.51	0.02
Mean visibility at flush point	1.46	0.23	1.83	0.18
CV of visibility at flush point	0.27	0.60	3.89	0.05
Migratory status	1.80	0.18	4.00	0.05
Body mass	1.92	0.17	6.31	0.01
Conspicuousness	3.06	0.08	22.03	<0.001
Activity height	1.89	0.17	46.80	<0.001

fect our inferences about the influences of other explanatory variables.

The year effects we detected demonstrate that avian responses to intrusion during one breeding season may not be the same as those in other breeding seasons. Consequently, analysis of the effects of intrusion should be based on multiple years of response data that involve the range of physical and biological conditions of interest. Contrary to studies of other bird species (Knight and Cole 1995, Gutzwiller and Marcum 1997), seasonal and daily timing of intrusion did not affect detectability period or approach distance. Evidently, the timing of our intrusions during the breeding season and during the day did not influence tolerance to an approaching person under the conditions and for the species we examined.

The positive relation between detectability period and number of nearby conspecifics indicates that birds were less tolerant of intrusion when they were in smaller conspecific groups. Solitary individuals or those in smaller groups were evidently more wary of potential predation by the intruder than were individuals in larger groups. This is consistent with numerous observations that as group size increases, individual birds in a feeding group spend less time being vigilant for predators (Lima and Dill 1990). Birds in larger groups also may be more tolerant of an approaching human if they are members of flocks that formed at sites with abundant food, where birds would benefit by remaining nearby (Greig-Smith 1981). These group-size results differ from those found in studies of some other species, wherein intrusion tolerance was usually lower for birds in larger groups (Knight and Cole 1995). Our group sizes (Table 2) were smaller than the group sizes (dozens to hundreds of individuals) typically involved in previous studies. Many bird species exhibit reduced vigilance for predators when feeding with other species (Pravosudov and Grubb 1995). Thus, we might expect that detectability period would increase and approach distance would decrease with heterospecific group size, but we found no evidence for this, indicating that number of nearby heterospecific individuals did not affect tolerance for intrusion.

For some species, vegetation situated between an intruder and a bird can increase tolerance to intrusion (Knight and Temple 1995b), but in the present study vegetation density and its vari-

ability around the intruder (observation point) and bird (flush point) did not influence tolerance. Using experimental intrusions, Burger and Gochfeld (1991) found that migrants were less tolerant of intruders than were residents. Klein et al. (1995) found similar results in an observational study involving responses to walking intruders and visitors in vehicles. For the species we studied, migratory status did not influence detectability period or approach distance. However, our assessment of the effect of migratory status on intrusion tolerance was limited because it involved only one migrant species (Table 1); a more thorough analysis would involve more migrant species. In previous studies, larger species have exhibited less tolerance to intrusion than smaller species (Cooke 1980, Humphrey et al. 1987, Holmes et al. 1993), but we found no significant effect of body mass on detectability period or approach distance, indicating that the occurrence of body-size effects on intrusion tolerance can vary with the set of species studied. The range of body sizes we studied was smaller than ranges analyzed by others who found effects (Cooke 1980, Humphrey et al. 1987, Holmes et al. 1993), so the detection of body-size effects also may depend upon the range of body sizes involved.

The positive relation between approach distance and conspicuousness indicates that species with brighter or more-contrasting colors had longer approach distances, implying that such species were less tolerant of intrusion. Conspicuous species may instinctively flush sooner during the approach of a potential predator because they are more detectable than inconspicuous species. The unprofitable-prey hypothesis predicts that conspicuous species may experience less avian predation than inconspicuous species because their bright or contrasting colors signal unprofitability (Götmark and Unger 1994). For the advantage of lower predation rates to be realized, however, conspicuous birds should evade predators more effectively (Götmark and Unger 1994). We found that more-conspicuous species had longer approach distances, which is consistent with the expectation that conspicuous birds should be more evasive toward potential predators. Species that are active closer to the ground during the breeding season had longer approach distances, indicating that they were less tolerant of intruders than were species that were active higher above the ground. Species with lower ac-

tivity heights were apparently more wary of the threat of predation that the intruder's presence may have represented.

Differences between relations reported in the present analysis and in the literature demonstrate that intrusion tolerance can be species- and context-dependent. Yet, efforts to discover principles or relations that apply across broad arrays of conditions and bird species should continue because such principles would be valuable for anticipating the conditions and species for which intrusion may be detrimental. Intrusion-induced behaviors such as nest abandonment and decreased nest attentiveness have led to reduced reproduction and survival (Götmark 1992, Gutzwiller 1995) in species that were intolerant of intrusion. To the extent that intrusion tolerance is linked to effects on reproduction and survival, knowledge of the factors that govern tolerance may be helpful for preventing or reducing impacts on reproduction and survival.

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