

# WILDLIFE BIOLOGY

## Research article

### Mallard response to experimental human disturbance on sanctuary areas is mediated by hunting

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Wildlife managers often provide spatial sanctuaries for wildlife to escape both lethal (e.g. hunting) and non-lethal (e.g. non-consumptive recreation) human disturbance. However, as societal interest in outdoor recreation continues to climb, many areas face added pressure to allow recreation, yet studies increasingly demonstrate negative effects of outdoor recreation on wildlife. As such, an understanding of how wildlife respond to human activities is essential to develop sustainable outdoor recreation guidelines to preserve multiple benefits for humans, while simultaneously protecting wildlife populations and fitness. We examined GPS-marked mallard responses to three experimental disturbances meant to mimic recreation that could theoretically occur on waterfowl sanctuaries during 1 November–28 February 2019–2022. We evaluated effects on movement, space use, and site fidelity and expected that repeated disturbance would result in habituation. We further evaluated predictions of the risk–disturbance hypothesis, whereby we predicted greater behavioral responses during the hunting period and to more intense stimuli. We conducted 140 covered vehicle (e.g. truck), 40 pedestrian, and 43 uncovered vehicle (e.g. ATV) disturbances across 10 sanctuaries, exposing 195 mallards to  $\geq 1$  disturbance (median = 2, range = 1–12). Diurnal sanctuary use exceeded 83% of proportional use regardless of period; however, mallards only decreased sanctuary use when disturbed before the hunting period with an uncovered vehicle. Besides immediate increases in hourly movements on mornings mallards received pedestrian and uncovered vehicle disturbances, disturbed mallards displayed minimal changes in hourly movements. At the diel scale, pedestrians elicited the greatest responses; space use doubled for disturbed birds during pre-hunt and early-hunt periods. In contrast, vehicle disturbances decreased movement but only outside the hunting period. Repeated disturbance caused gradual declines in space use: mallards used 12% less space with each additional disturbance during hunting. Constrained



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behavioral responses and unchanged sanctuary fidelity after disturbance during hunting season suggests the limited availability of alternative safe areas constrained mallard responses to disturbances.

Keywords: anthropogenic disturbance, dynamic landscapes of fear (LOF), GPS-telemetry, hunting, sanctuary, waterfowl

## Introduction

A comprehensive understanding of behavioral responses by animals to various forms and intensities of human recreation (i.e. disturbance) is useful to effectively balance wildlife conservation with societal demands for accessible outdoor recreation (Larson et al. 2016). A dominant model for understanding behavioral responses of animals to human-induced disturbance is through stimulus–response studies, which involve an external stimulus (e.g. a person) and a response on part of the animal (e.g. escape behavior), with various internal and external influences mediating the response (Blumstein 2006, Weston et al. 2012). For instance, researchers have monitored the probability or severity of animal behavioral responses relative to human recreational stimuli, which has led to important recommendations for optimal wildlife sanctuary designs (Madsen and Fox 1995) and spatial delineation of protective buffers and human exclusion zones for the protection of wildlife in natural areas (Fernández-Juricic et al. 2005, Livezey et al. 2016).

The risk–disturbance hypothesis provides a well-supported theoretical underpinning for understanding and predicting animal responses to human activity (Frid and Dill 2002). The risk–disturbance hypothesis posits that animals perceive and respond to human activities as they would natural predators. Therefore, the probability and intensity of the response depend on an inherent trade-off between risk avoidance (i.e. in this case, human avoidance) with other fitness-enhancing activities, such as foraging, mating, or rearing young (Clinchy et al. 2016, Suraci et al. 2019). Heightened anti-predator responses, even to non-threatening human disturbance, can impose fitness consequences that are potentially as detrimental to populations as direct effects (i.e. natural predation or harvest). For example, increased vigilance (Jayakody et al. 2008, Ciuti et al. 2012, Paton et al. 2017), increased flight initiation distances (Madsen and Fox 1995, Sreekar and Goodale 2015), and altered movement or space-use patterns (Beauchesne et al. 2014, Tucker et al. 2018) may carry severe costs to individuals by artificially increasing energy expenditure or through lost foraging or mating opportunities (reviewed by Frid and Dill 2002, Tablado and Jenni 2017). Although multiple studies have described wildlife responses to a gradient of human disturbance (Pease et al. 2005, Dooley et al. 2010, McLeod et al. 2013, Mayer et al. 2021), few general patterns tend to emerge, presumably due to the context-dependent nature with which animals perceive and respond to human disturbances (e.g. inter- and intra-individual and species variation; Tablado and Jenni 2017).

The probability or severity of wildlife responses to human activities likely depend on background levels of

human-induced risk in the environment (Courbin et al. 2022, Meisingset et al. 2022). For instance, when prey animals experience several co-occurring sources of human risk with differing degrees of lethality (e.g. birdwatching versus hunting), prey abilities necessary to adjust the strength of response to disturbance stimuli are likely exceeded. As such, empirical studies demonstrate increased sensitivity of wildlife to benign sources of human disturbance (e.g. hikers, passing vehicles) during hunting periods (Madsen and Fox 1995, Paton et al. 2017, Westekemper et al. 2018, Courbin et al. 2022, Meisingset et al. 2022), perhaps due to a broad perception of humans as sources of lethal risk during these times. However, increased responsiveness to benign disturbance may facilitate predation if the disturbance elicits movements or shifts in resource use that increase exposure to hunters or natural predators (Crosmarty et al. 2012, Neilson and Bouton 2017, Gehr et al. 2018).

To inform management decisions, wildlife managers and agencies would benefit from an understanding of whether wildlife habituate to human-induced disturbance. Habituation is a learning process leading to decreased responsiveness to a repeated stimulus that is often considered adaptive, because it makes it less likely that individuals will continue to respond to benign stimuli (Rankin et al. 2009, Blumstein 2016). There are numerous situations where one might wish to promote habituation (i.e. reduced response to repeated exposure) to human-induced disturbance in wildlife, as in the case of installing a new hiking trail or opening a formerly closed area to non-consumptive recreational access. Although some stimulus–response studies indicate wildlife appear to habituate to some forms of repeated anthropogenic disturbances, responsiveness varies within and among species (Stankowich 2008, Bejder et al. 2009, Lewis et al. 2021). Furthermore, most studies have not evaluated habituation using marked individuals, limiting the inference to inform management decisions (Blumstein 2016).

Wildlife sensitivity to human disturbance also depends on availability of alternative safe areas (Rode et al. 2006, Bonnot et al. 2013, Ericsson et al. 2015, Carbillet et al. 2020). For example, wildlife managers often restrict hunter access to portions of the landscape (i.e. spatial sanctuary) or during certain times (i.e. temporal sanctuary; Tolon et al. 2009, Casazza et al. 2012) to limit disturbance to and harvest mortality of hunted species. Consequently, hunted species often increase diurnal use of sanctuaries during hunting seasons, exploiting hunted areas nocturnally when hunters are inactive (Crosmarty et al. 2012, Visscher et al. 2017, Shirkey et al. 2020, Palmer et al. 2022). However, increased diurnal sanctuary use largely precludes hunters and wildlife viewers from accessing wildlife (Casazza et al. 2012, Shirkey et al. 2020,

McDuie et al. 2021). Consequently, there is growing public pressure to increase recreation, particularly non-consumptive uses like hiking and wildlife viewing, in areas traditionally managed as spatial sanctuary (Devers et al. 2017, Responsive Management and National Shooting Sports Foundation 2017, USDOI 2017). Evaluating wildlife responses to such novel disturbances on spatial sanctuaries is therefore an urgent conservation priority but must be couched within the broader spatio-temporal dynamics of human-induced risk at landscape scales and the potential for wildlife to habituate or sensitize to human-induced disturbance (Bejder et al. 2009, Kerbiriou et al. 2009, Blumstein 2016).

We conducted experimental disturbances on state and federal waterfowl sanctuaries in western Tennessee, USA, to evaluate mallard *Anas platyrhynchos* behavioral responses to human disturbance in a critical wintering region. Sanctuaries in this region are closed to public access during winter to provide refuge from hunting disturbance but face growing pressure for increased recreational use (Hagy et al. 2017, Blake-Bradshaw et al. 2023). We simulated three types of human disturbance of increasing intensity that mimicked non-consumptive human activities that may be permissible on waterfowl sanctuaries: 1) disturbance in a covered vehicle that simulated auto tours for waterbird viewing; 2) a walking pedestrian disturbance which represented bird-watching activities; and (3) an uncovered vehicle disturbance through

the wetlands that represented ATV or boating recreation (Fig. 1A). We evaluated effects of our experimental sanctuary disturbances on mallard movement distances, space use, and sanctuary residency using GPS telemetry. Importantly, we evaluated how hunting risk mediated mallard responses to disturbance and tested for evidence of behavioral habituation. Based on the risk–disturbance hypothesis, we expected mallards to exhibit stronger responses to disturbance during hunting season and to more threatening stimuli (Fig. 1B). We also expected repeated disturbance to result in habituation and progressively weaker responses (Fig. 1C).

## Material and methods

### Study area

Our study took place in western Tennessee, USA, within a portion of the Lower Mississippi Alluvial Valley as well as the Obion and Forked Deer river floodplains (~ 6000 km<sup>2</sup>; ~150 m ASL; Fig. 2). The landscape was mostly flat (~ 123 m) with some hilly terrain along the Mississippi River floodplain (e.g. 15–61 m ridges of loess). Areas within river floodplains contained wetlands, and river corridors were dominated by willow (*Salix* spp.), maple (*Acer* spp.), and ash (*Fraxinus* spp.). Hilly land and river corridors were forested; otherwise,

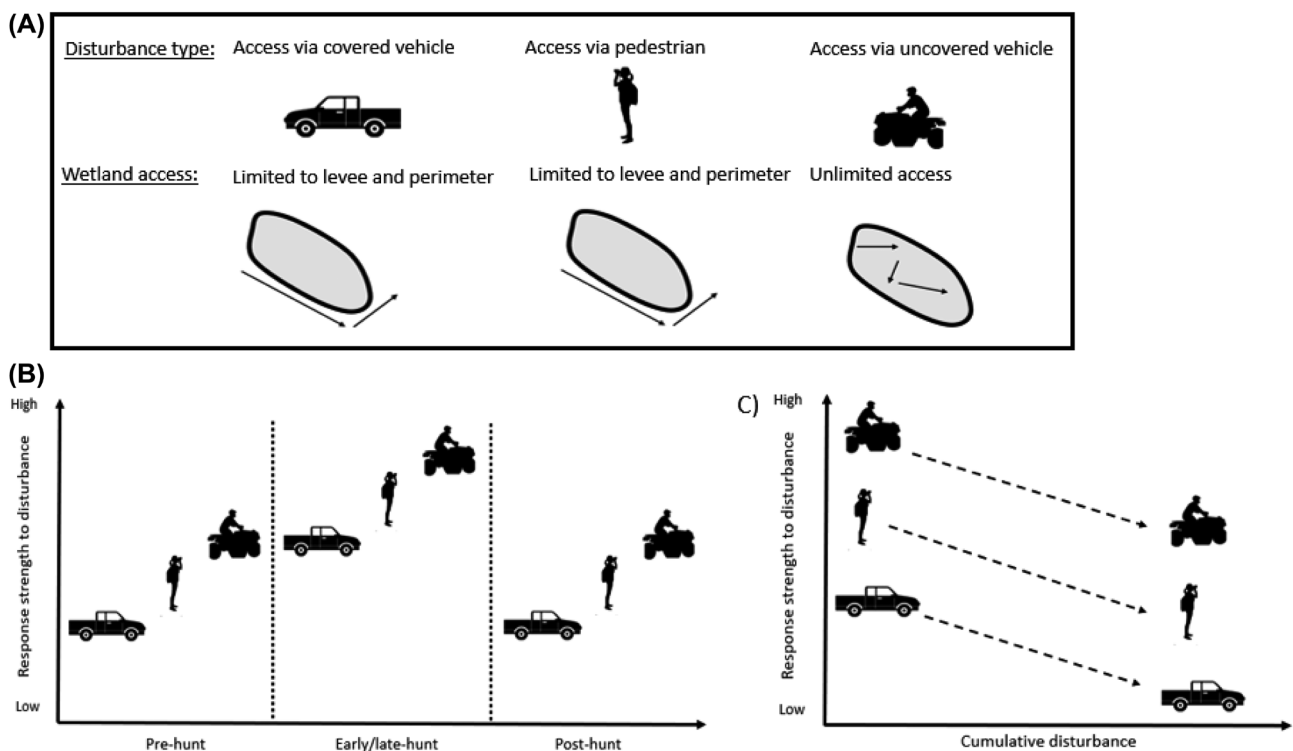


Figure 1. Schematic of and predicted mallard responses to disturbance treatments which occurred on waterfowl sanctuaries in western Tennessee, USA, November–January during 2019–2022. (A) Disturbance treatments by increasing intensity (low, medium, and high) and access to wetland units. (B) We predict mallards should respond to higher intensity disturbances more; we further predict mallards would greatly increase response to disturbance during both the early- and late-hunt periods; (C) we predict mallards exposed to repeated disturbance (cumulative disturbance) on sanctuaries will decrease responsiveness (e.g. habituate).

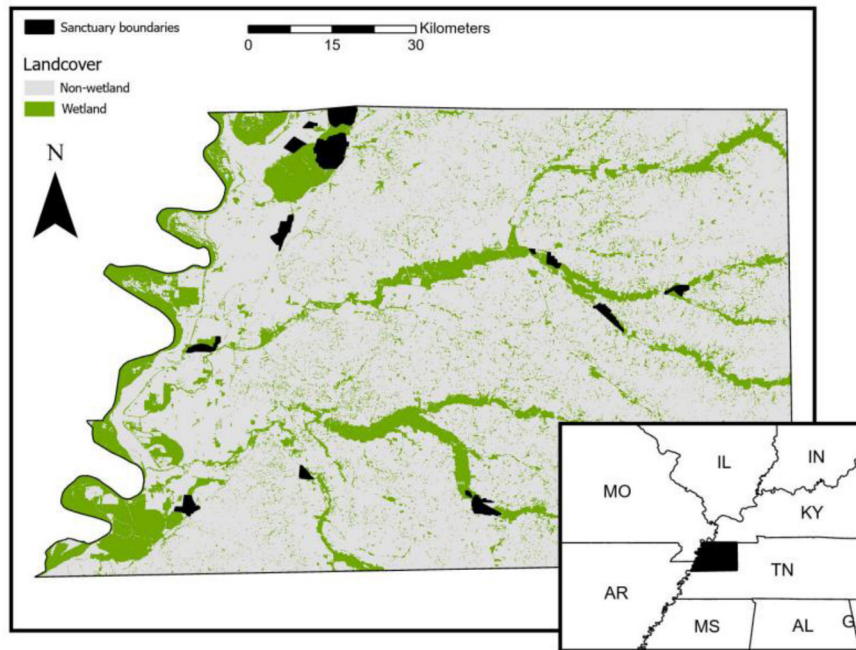


Figure 2. Location of sanctuary boundaries and landcover types in the northwestern corner of Tennessee, USA, November–January during 2019–2022. Landcover for this map was extracted from the 2020 Cropland data layer (USDA 2020) and reclassified into wetland (herbaceous wetlands, woody wetlands, open water) and non-wetland.

agriculture was the dominant land use. Western Tennessee has warm humid summers (mean July temperature  $\approx 28^{\circ}\text{C}$ ), wet mild winters (mean January temperatures  $\sim 4^{\circ}\text{C}$ ), and  $\sim 140$  cm of annual precipitation (USFWS 2006). Winter and early spring are the wettest times of year, and summer and early fall the driest (Brown et al. 1973).

The study area contained three federal waterfowl sanctuaries and seven state-owned sanctuaries, including: Chickasaw National Wildlife Refuge (NWR), Lake Isom NWR, Reelfoot NWR, Bean Switch Refuge, Black Bayou Refuge, Hop-In Refuge, Horns Bluff Refuge, Lake Lauderdale Refuge, Maness Swamp Refuge, and White Lake Refuge. Sanctuaries varied in size (median = 494 ha, range = 260–3384 ha) and distances apart (median = 8.5 km, range = 1–22 km; Fig. 2). Because Black Bayou Refuge and Reelfoot NWR were  $< 1.5$  km apart, we considered them one sanctuary. These sanctuaries hosted abundant waterfowl throughout the hunting season during our study (Hagy et al. 2022, TWRA 2023). Hunting and other public access (i.e. vehicular and foot traffic) were prohibited on sanctuaries on or before 15 November and until 1 March each year. Therefore, spatial sanctuaries in our study prohibited all human access during the wintering period, except infrequent maintenance checks by agency staff. Additionally, sanctuaries contained food resources, including annual seeds produced via moist-soil management and planted agricultural crops (e.g. corn *Zea mays*, millet [*Echinochloa* spp.; *Urochloa* spp.], and rice *Oryza sativa*). In addition to sanctuaries and other managed public lands, private landowners provide extensive, often impounded, habitat and food resources across the study area (Highway 2022).

The waterfowl hunting season lasted 60 days, with an opening weekend in mid-November for Reelfoot Lake and late November for the remainder of the study area. The season then closed until early December when it reopened and remained open until the end of January each year (Supporting information). Within our study area, waterfowl hunters hunt almost exclusively out of stationary blinds (Poudyal and Shrestha 2020), and most of the blinds in our study area were occupied by waterfowl hunters, indicating relatively stable hunter density over time (Masto 2023).

### Animal capture and telemetry

We captured mallards using a combination of swim-in traps, confusion traps, and rocket-nets at eight sanctuaries in western Tennessee, USA, from November through February 2019–2022 (Wunz 1984, Evrard and Bacon 1998). We banded all ducks with USGS standard aluminum tarsal bands. We recorded mass ( $\pm 1$  g) and determined age and sex of mallards based on cloacal inversion, wing plumage, and bill color (Carney 1992). We assigned mallards to either juvenile or adult age classes. We attached 20 g solar rechargeable and remotely programmable OrniTrack Global Positioning System-Global System transmitters (GPS-GSM; Ornitela, UAB Švitrigailos, Vilnius, Lithuania) to mallards weighing  $\geq 1000$  g (i.e. transmitters were  $\leq 2.5\%$  of total body mass) to ensure that deployment package remained below recommended body weight limits (3–5%; Fair et al. 2010). We attached transmitters via dorsally mounted body harnesses made of automotive moisture-wicking elastic ribbon (Masto et al. 2022). Completed harnesses had two body



loops knotted and sealed with cyanoacrylic glue above the keel and across the abdomen of the bird (McDuie et al. 2019, Masto et al. 2022). Total package of GPS–GSM transmitter and harnesses at the time of deployment weighed ~ 22 g, and average location error based on GPS fix rate and median positional error rate was 23.5 (Frair et al. 2010, Overton, USGS, pers. comm.).

We programed transmitters to record hourly GPS locations when battery levels were > 25% and record a GPS location every 36 h when battery levels were < 25% to allow battery recharge. During the first year of our study, we also collected GPS locations at 2-h intervals depending on battery levels. For our analyses, we filtered our data to either 1- or 2-h fixes, as these fix-rates do not bias space use calculations (Cohen et al. 2018). We censored the first four days after deployment to allow acclimation to the GPS unit (Cox and Afton 1998). We monitored individuals until transmitter failure (i.e. battery malfunction, loss of cellular service), an individual was reported as harvested by a hunter, or we identified that an individual died via examination of tri-axial accelerometer graphs.

## Behavioral metrics

We evaluated the influence of disturbance on mallard movements and probability of sanctuary use at the hourly scale during the diurnal period (Table 1). We also evaluated the influence of disturbance on mallard movements, space use, and sanctuary fidelity across diel periods (i.e. diurnal versus nocturnal; Table 1). We defined the diurnal period as legal shooting hours, spanning 30 min before sunrise until sunset and the nocturnal period as sunset until 30 min prior to sunrise. We calculated diel distance moved (km) by summing step lengths during each diel period each day for each individual mallard (Table 1). To assess space use, we estimated utilization distributions (UDs) using a third-generation estimator, the dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012). The dBBMM requires several parameters to estimate a Brownian-Bridge UD: a time index series of animal locations, an estimate of mean telemetry error for each location and an estimate of Brownian motion variance ( $s^2m$ ), which is a measure of irregularity of an animal's movement path between two locations and a function of the animal's behavior (Kranstauber et al. 2012).

The dBBMM accounts for changes in animal behavior (e.g. foraging, resting) over time by estimating a unique  $s^2m$  value for each time step between GPS locations (Gurarie et al. 2009). Following recommendations of Kranstauber et al. (2012), we chose a window size based on the temporal resolution of each track and our prior assumptions of the timescale of behavioral shifts. Specifically, we parameterized dBBMMs using our average location error of 23.5 m, a moderate window size of 15 (equivalent to 15 h) and a moderate margin of 5 to identify breakpoints. We bursted the dBBMMs by diel period and extracted 50% UD for each individual-diel period-date combination to represent the core area used by mallards during each diel period (Table 1; Kranstauber et al. 2012, 2023). Lastly, we evaluated sanctuary use and fidelity by calculating the proportion of an individual's locations on a sanctuary during the day and night (Table 1). Because we were interested in fidelity to the disturbed sanctuary, locations on another sanctuary following a disturbance event were not included in our calculation of proportion sanctuary use.

## Data filtering

We removed mallards that did not use sanctuaries in the diurnal period during our study period from our analyses because mallards needed to be on a sanctuary to receive disturbance treatments, and inclusion of these birds could bias comparisons of sanctuary use or movement. Specifically, we compared disturbed mallard responses to undisturbed individuals that had at least one location on a sanctuary between 05:00 and 11:00 h for a given day. Filtering our data in this manner allowed us to elucidate to what extent disturbing sanctuaries affected mallard movements, space use, and sanctuary site fidelity in a more appropriate manner, because the 'control' birds (i.e. mallards that were not disturbed but were located on sanctuary) would at least be available to disturbance and more likely to have similar daily activity patterns than mallards that did not use sanctuary.

## Experimental disturbances

We conducted three distinct disturbance treatments along a gradient of increasing intensity (Blake-Bradshaw et al. 2023, Fig. 1). Disturbance treatments were separated by at least five days, so they were reasonably isolated and independent

Table 1. Group, metric, and description for behavioral metric response variables used to evaluate mallard *Anas platyrhynchos* response to disturbance on state and federal waterfowl sanctuary areas in western Tennessee, USA, during winter (1 November–28 February) 2019–2022.

Group	Metric	Temporal scale	Description
Movement	Distance moved	Hourly	Hourly step length (km)
		Diel	Total distance in kilometers (km) per date/time of day combination
Space use	Utilization distribution	Diel	Probability that an animal is found at a given point in space. The 50% (core area) UD are calculated via a Dynamic Brownian Bridge per date/time of day combination
Sanctuary fidelity	Probability of locations on sanctuary	Hourly	Probability that a mallard was located on a sanctuary
	Proportion of locations on sanctuary	Diel	Proportion of locations on sanctuary per date/time of day combination

events allowed birds to resume normal activities (Dooley et al. 2010). Disturbance treatments lasted approximately one hour and occurred primarily between 07:00 and 09:00 h. The treatment representing the lowest intensity of disturbance was a waterfowl survey conducted from a covered vehicle (i.e. truck; Pease et al. 2005, McLeod et al. 2013; Fig. 1). Observers drove predetermined routes along roads or levees, with vantage points to estimate waterfowl abundance. This treatment approximated an auto-tour for waterfowl watching. The length of routes differed among sanctuaries based on their size and vegetative cover (e.g. forested versus open water wetlands). An intermediate intensity disturbance treatment mimicked disturbance from a pedestrian engaged in a slow and methodical activity, such as bird-watching or recreational hiking (McLeod et al. 2013, Guay et al. 2019; Fig. 1). Two observers walked separate routes along levees at normal walking speed (i.e. 4.8 km h<sup>-1</sup>) and walked the same routes at each visit. The highest intensity disturbance treatment was driving an uncovered vehicle, either an all-terrain vehicle (ATV) or an outboard motorboat, into wetlands (Havera et al. 1992, Madsen and Fox 1995, Knapton et al. 2000; Fig. 1). We maintained speed of motorized vehicles to approximately 16 km h<sup>-1</sup> for 10 min, stopped for 5 min, and repeated until one hour elapsed. This high-intensity treatment best approximated high-disturbance events such as recreational boating and ATV riding. The covered vehicle disturbance occurred approximately twice a month around the start of and mid-point of the month, whereas the pedestrian and uncovered vehicle disturbances occurred approximately once a month.

We determined whether an individual received a disturbance treatment by overlaying mallard locations with sanctuary boundaries and comparing timestamps. If a mallard had  $\geq 1$  location on the disturbed sanctuary between sunrise and the end of the disturbance treatment, we designated that the

individual received the disturbance treatment. Our determination of whether mallards received a disturbance treatment was reasonable because waterfowl typically conduct flights before dawn and after dusk, spending the majority of time in a limited area each day (i.e. sanctuary, wetland; McDuie et al. 2019, 2021).

## Model formulation and statistical analyses

At the hourly scale, we log-transformed the distance moved response variable to better approximate a Gaussian distribution, and we modeled hourly sanctuary use using a binomial distribution (Table 2). At the diel-scale, we also log-transformed distance moved and space use response variables to better approximate a Gaussian distribution. We modeled diel proportional sanctuary use by fitting a zero-one-inflated beta regression, which allows both 0 and 1s in our outcome for when an individual mallard did not use sanctuary or used only sanctuary, respectively (Ospina and Ferrari 2010, 2012; Table 2). We conducted hierarchical modeling within a Bayesian framework using the 'brms' package (Bürkner 2017, 2018). At the hourly scale, we included hour of day as a fixed effect to account for inherent differences in movements and sanctuary use within a day. At the diel-scale, we similarly included diel period as a fixed additive effect in all models to account for inherent differences in movements and activity between these periods. We created a categorical variable representing the distinct disturbance treatment (none, covered vehicle, pedestrian, and uncovered vehicle). We then created a variable representing cumulative disturbance exposures, across all treatment types each mallard experienced at a given point in time. To assess how regional risk influenced responses to disturbance, we calculated a variable representing hunting period (pre-hunt, early-hunt, late-hunt, post-hunt).

Table 2. Overview of analyses separated by objectives: 1) behavioral responses to disturbance treatments, and 2) evidence of habituation or sensitization of mallards (*Anas platyrhynchos*) to disturbance treatments in western Tennessee, USA, during 1 November–28 February 2019–2022. We included diel period in all diel-scale models and hour of day (0000–2300) in all hourly models as additive effects to account for inherent differences in movements and activity between these times. Note, we omitted sanctuary ID as a random effect for the hourly probability on sanctuary model to achieve model convergence. <sup>a</sup>Rather than running a 3-way interaction, we split the data into hunt and non-hunt periods and ran the hourly models separately.

Objective	Response variable	Fixed effects	Random effects	Temporal scale	Model link
1	Distance moved	Disturbance type $\times$ hour of day $\times$ hunting season <sup>a</sup>	Mallard ID, Sanctuary ID	Hourly	Gaussian
	Probability on sanctuary	Disturbance type $\times$ hour of day $\times$ hunting season <sup>a</sup>	Mallard ID	Hourly	Binomial
	Distance moved	Disturbance type $\times$ hunting season	Mallard ID, Sanctuary ID	Diel	Gaussian
	Space use	Disturbance type $\times$ hunting season	Mallard ID, Sanctuary ID	Diel	Gaussian
	Proportion sanctuary use	Disturbance type $\times$ hunting season	Mallard ID, Sanctuary ID	Diel	Zero-one-inflated beta
2	Distance moved	Cumulative disturbance $\times$ hunting season	Mallard ID, Sanctuary ID	Diel	Gaussian
	Space use	Cumulative disturbance $\times$ hunting season	Mallard ID, Sanctuary ID	Diel	Gaussian
	Proportion sanctuary use	Cumulative disturbance $\times$ hunting season	Mallard ID, Sanctuary ID	Diel	Zero-one-inflated beta

Each period approximated one month (pre-hunt was during November, early-hunt during December, late-hunt during January, and post-hunt during February). To account for repeated measures from individual mallards, we specified each individual as a random effect (Table 2). Additionally, we treated individual sanctuaries as a separate random intercept to account for differences in mallard movements, space use, and sanctuary use that may vary depending on sanctuary characteristics (e.g. size, cover types; Table 2). Accounting for variation among individuals and sanctuaries allowed us to isolate the average effects of experimental disturbance treatments on mallard behaviors.

To assess how background risk (i.e. hunting period) affected behavioral responses to disturbance, we first evaluated immediate responses by modeling hourly distance moved and hourly probability of sanctuary use as a function of disturbance type (none, covered vehicle, pedestrian, uncovered vehicle), hour of the day (0000–2300) and their interaction, with individual and sanctuary as separate random intercepts (Table 2). Rather than investigate a 3-way interaction, we split our data into a hunt (early- and late-hunt) and non-hunt period (pre-hunt and post-hunt) and ran separate hourly models (Table 2). We then modeled each diel-scale behavioral metric as a function of disturbance type (none, covered vehicle, pedestrian, uncovered vehicle), hunting period (pre-hunt, early-hunt, late-hunt, post-hunt), and their interaction, with individual and sanctuary as separate random intercepts (Table 2). To test for habituation, we modeled changes in behavioral responses to disturbance as a function of an individual's cumulative number of prior disturbances. Because cumulative exposures increased over time and were unbalanced across hunting periods, we similarly collapsed the pre-hunt and post-hunt periods into a non-hunt period and the early-hunt and late-hunt periods into a hunt period for the cumulative disturbance models. We filtered our data to include only days individual mallards were disturbed. We then ran models for each behavioral metric with an interaction between hunting season (i.e. hunt and non-hunt) and cumulative disturbance to allow for the influence of cumulative disturbance to differ depending on background risk (i.e. hunting period; Table 2).

Our sampling design and multivariate approach are appropriate because sample sizes exceed those generated from common rules of thumb (Green 1991), are greater than suitable sample sizes calculated using meta-analysis and simulation-based approaches (Forcino et al. 2015), and are likely appropriate given the ecology of our study species (Lamb et al. 2023). To best achieve population-level representation and capture spatiotemporal differences in behavioral responses to disturbance, we marked mallards across all 10 sanctuaries located within our study area and across multiple years (i.e. 2019–2022; Lamb et al. 2023). Additionally, the vast majority of waterfowl were located on waterfowl sanctuaries throughout the duration of our study (i.e. observed via weekly aerial surveys; Masto USFWS pers. comm.), suggesting that our marked sample of mallards captured on sanctuaries

likely represented the greater population well. According to Lamb et al. (2023), sampling power increases, and thus smaller sample sizes are required, for gregarious species that stage and forage in large flocks during non-breeding periods, all conditions met by our study species (i.e. common terns *Sterna hirundo* [Lamb et al. 2023]; mallards [current study]). We used weakly informative priors (Lemoine 2019) and conducted prior predictive checks to evaluate whether priors were appropriate (Gabry et al. 2019, Gabry and Mahr 2022). We fit models with four Markov chain Monte Carlo chains and 6000 iterations for each chain (1000 burn-in iterations, thin=1). We checked model convergence by inspecting trace plots and the Gelman Rubin statistic ( $\hat{R}$ ) and assessed model fit visually via posterior predictive diagnostic plots and the Bayesian  $R^2$  (Bürkner 2017, Gelman et al. 2019, Gabry and Mahr 2022). We examined 85% credible intervals to evaluate the direction and strength of effects (Arnold 2010, Sutherland et al. 2023). All analyses were conducted in R ver. 4.2.2 (www.r-project.org).

## Results

We conducted 223 disturbance treatments across 10 sanctuaries, of which 140 were in a covered vehicle, 40 were pedestrian disturbances, and 43 were in an uncovered vehicle. We marked 444 mallards with GPS transmitters, of which 84 were adult females, 156 were adult males, 107 were juvenile females, and 97 were juvenile males. Sixty-four mallards (14%) did not use sanctuaries after marking and were removed from further analysis. One hundred and ninety-five mallards (44%) received at least one disturbance treatment, resulting in 629 total disturbance encounters. The median number of disturbance encounters was 2 (range=1–12) for mallards disturbed  $\geq 1$  time. Disturbed mallards rarely switched to other sanctuaries; only 1.6% of disturbance encounters resulted in an individual switching to another sanctuary that day. Posterior predictive checks indicated models fit the data well (Supporting information). Bayesian  $R^2$  and standard deviation for random effects can be viewed in the Supporting information.

### Hourly sanctuary use

Mallards showed a clear dichotomous pattern in hourly sanctuary use. Mallards greatly increased the use of sanctuary just before and following the diurnal period (e.g. 0400–1700) during both the hunt and non-hunt seasons (Fig. 3A–B). Furthermore, the probability of sanctuary use was greater for disturbed mallards than undisturbed mallards across all disturbance treatment and hunting periods, but there was greater variation in sanctuary use by disturbed mallards outside the hunting period (Fig. 3A–B; Supporting information). Notably, sanctuary use only declined (~10% decrease between 08:00 and 16:00 h) in response to the highest intensity uncovered vehicle disturbance outside of the hunting period (Fig. 3B, Supporting information).

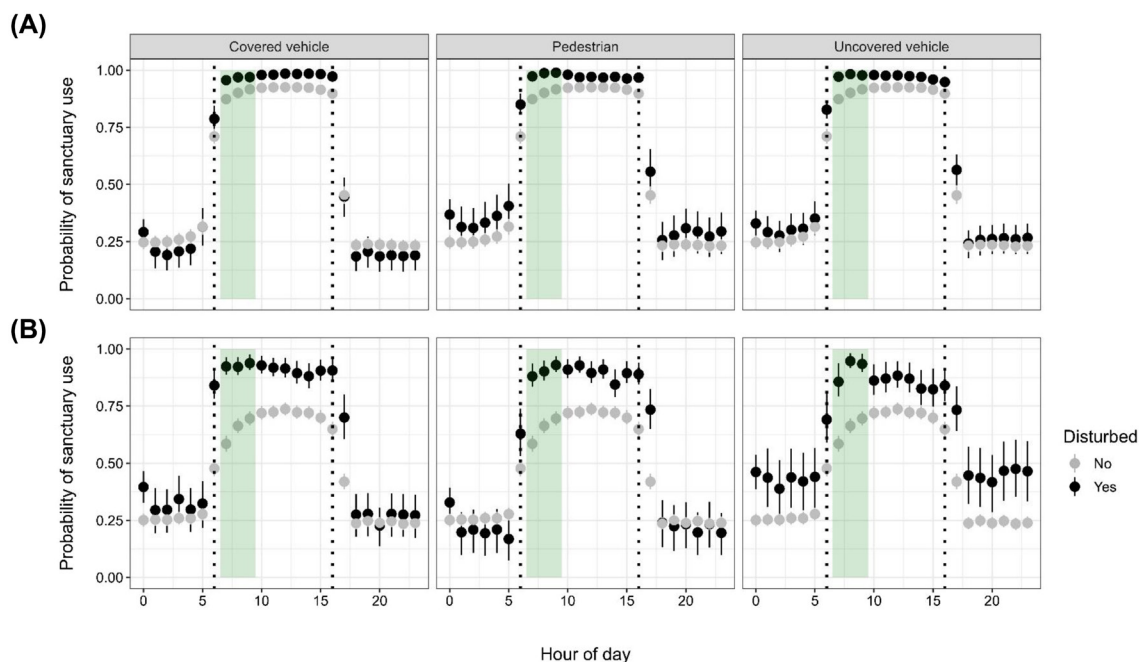


Figure 3. Model-predicted probability of sanctuary use by mallards *Anas platyrhynchos* depending on disturbance treatment and hour of day (5=05:00, 10=10:00, 15=15:00) split by hunting period: panel (A) probability of sanctuary use during the hunting period; (B) probability of sanctuary use during the non-hunting period. Disturbances occurring primarily between 07:00 and 09:00 indicated by shaded green region, and vertical dashed lines indicate approximate sunrise and sunset times. The 85% credible intervals are shown as vertical bars. The study occurred in western Tennessee, USA, during 1 November–28 February 2019–2022.

### Hourly distance moved

Hourly mallard movements were similar across both hunting periods. Besides increased movement around sunrise and sunset, as mallards moved to and from sanctuaries, mallards rarely made hourly movements > 0.03 km (Fig. 4A–B, Supporting information). Experimental disturbance impacted hourly mallard movements in a context-dependent manner. For instance, during the hunt period (early-hunt and late-hunt), mallards decreased hourly movements by 24.4–51.8% during the mid-morning to afternoon (i.e. 10:00–15:00) in response to the lowest-intensity covered vehicle disturbance (Fig. 4A, Supporting information). In contrast, however, mallards increased hourly movements on mornings when disturbed by the pedestrian or uncovered vehicle disturbance during hunting. For instance, in response to the pedestrian disturbance, mallards moved 40.1–107.5% more than undisturbed mallards until late morning (i.e. 07:00–12:00) when hourly movements returned to reference levels. Similarly, mallards moved 27.1–73.3% more than undisturbed mallards in response to the high-intensity uncovered vehicle disturbance during morning (i.e. ~07:00–09:00 h) with hourly movements returning to reference levels thereafter. Then, during the non-hunt period (pre-hunt and post-hunt), mallards show limited change in hourly distance moved when they received the low-intensity covered vehicle disturbance, but mallards that received the pedestrian or uncovered vehicle disturbance showed increased movement compared to undisturbed mallards (Fig. 4B, Supporting information). For

instance, mallards moved 153% more than undisturbed mallards on the morning of a pedestrian disturbance (i.e. 08:00), moved 60.0% more at mid-day (i.e. 12:00), and 71.6% more in the afternoon (i.e. 14:00; Fig. 4B, Supporting information). Lastly, in response to the highest-intensity disturbance, the uncovered vehicle, mallards moved 203.4% more than undisturbed mallards on the morning of the disturbance (i.e. 09:00; Fig. 4B, Supporting information). It should be noted, however, that while there were multiple interactions that were significant and reported here, actual changes in mallard movements in response to disturbance treatments on waterfowl sanctuaries appear relatively minimal as predicted changes in movement were < 0.07 km (range: 0.01–0.07 km; Fig. 4A–B; Supporting information).

### Diel sanctuary use

Mallards used sanctuaries extensively during daylight hours at the diel scale. For mallards that used sanctuary during our study, diurnal sanctuary use was high ( $\geq 83.9\%$ ) across all periods but decreased by 58.6% ( $\beta = -1.44$ ,  $SE = 0.03$ ) during nocturnal times (Fig. 5A, Supporting information). Mallards only reduced sanctuary use in response to the highest intensity disturbance, the uncovered vehicle, prior to the hunting period. Specifically, mallards disturbed by the uncovered vehicle during the pre-hunt period reduced sanctuary use by 7.1% ( $\beta = -1.02$ ,  $SE = 0.51$ ) relative to undisturbed mallards (Fig. 5A). Mallards increased sanctuary use slightly in response to cumulative disturbance; for every additional



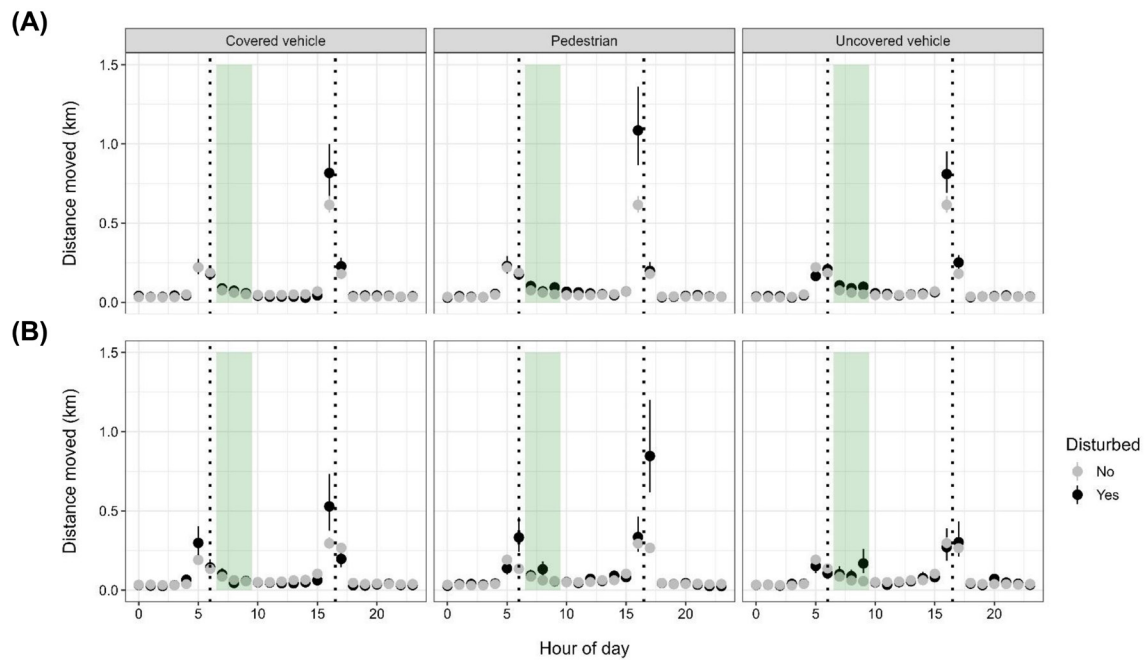


Figure 4. Model-predicted hourly distance moved (km) of mallards *Anas platyrhynchos* depending on disturbance treatment and hour of day (5 = 05:00, 10 = 10:00, 15 = 15:00) split by hunting period: panel (A) distance moved during the hunting period; (B) distance moved during the non-hunting period. Disturbances occurred primarily between 07:00 and 09:00 indicated by shaded green region, and vertical dashed lines indicate approximate sunrise and sunset times. The 85% credible intervals are shown as vertical bars. The study occurred in western Tennessee, USA, during 1 November–28 February 2019–2022.

disturbance encounter, mallards increased diel sanctuary use 0.3% ( $\beta = 0.04$ ,  $SE = 0.02$ ; Fig. 6A, Supporting information).

### Diel distance moved

Mallards moved more during the nocturnal period, averaging 15.0% ( $\beta = 0.14$ ,  $SE = 0.02$ ) greater distance moved (Supporting information). Distance moved increased over time. On average, mallards moved 1.7 km (85% CRI: 1.5–2.0) diurnally during the pre-hunt period, and moved 7.3% ( $\beta = 0.07$ ,  $SE = 0.03$ ) more during early-hunt, 16.2% ( $\beta = 0.15$ ,  $SE = 0.03$ ) more during late-hunt, and 19.8% ( $\beta = 0.18$ ,  $SE = 0.03$ ) more during post-hunt. Distance moved by mallards in response to disturbance differed across disturbance types and hunting seasons (Fig. 5B; Supporting information). Generally, mallards were most sensitive to the pedestrian disturbance (Fig. 5B); compared to undisturbed mallards, mallards disturbed by pedestrians moved 20.2% ( $\beta = 0.26$ ,  $SE = 0.11$ ) more during the late-hunt, and 18.1% ( $\beta = 0.23$ ,  $SE = 0.12$ ) more during the post-hunt period (Fig. 5B). Mallards disturbed during the early-hunt period had no change in distance moved (Fig. 5B; Supporting information). Moreover, the vehicle disturbances (i.e. covered and uncovered vehicle) resulted in decreased movement outside of the hunting periods. Compared to undisturbed mallards, mallards that received the covered vehicle disturbance moved 17.7% ( $\beta = -0.12$ ,  $SE = 0.06$ ) less during the post-hunt period. The uncovered vehicle also decreased distance moved; mallards moved 15.5% ( $\beta = -0.16$ ,  $SE = 0.11$ ) less

during the post-hunt period relative to undisturbed mallards (Fig. 5B). Lastly, cumulative disturbance did not influence diel distance moved, either within or outside of the hunting season (Fig. 6B; Supporting information).

### Diel space use

Mallard space use differed across the hunting seasons but was greatest during early-hunt; mallards used a core area of 15.2 ha (85% CRI = 11.7–19.9 ha) on average diurnally during the early-hunt period. Compared to late-hunt, mallards used 10.4% ( $\beta = -0.11$ ,  $SE = 0.05$ ) less space during the post-hunt, 23.4% ( $\beta = 0.21$ ,  $SE = 0.05$ ) more space during early-hunt, and 18.5% ( $\beta = 0.17$ ,  $SE = 0.08$ ) more space during pre-hunt (Fig. 5C; Supporting information). Mallards used 62.4% ( $\beta = -0.98$ ,  $SE = 0.04$ ) less space during the nocturnal period compared to the diurnal period (Supporting information). Disturbance typically resulted in greater space use, but effect sizes differed across disturbance treatments and hunting periods (Fig. 5C; Supporting information). Compared to undisturbed individuals, mallards that received the pedestrian disturbance during the pre-hunt and early-hunt periods increased space use the greatest, using 99.4% ( $\beta = 0.69$ ,  $SE = 0.36$ ) and 109.6% ( $\beta = 0.74$ ,  $SE = 0.23$ ) larger core areas, respectively (Fig. 5C). Mallard response to the uncovered vehicle differed depending on hunting period. During the pre-hunt period, mallards that received the uncovered vehicle disturbance used 37.5% ( $\beta = -0.76$ ,  $SE = 0.63$ ) less space than undisturbed mallards, but increased space use by

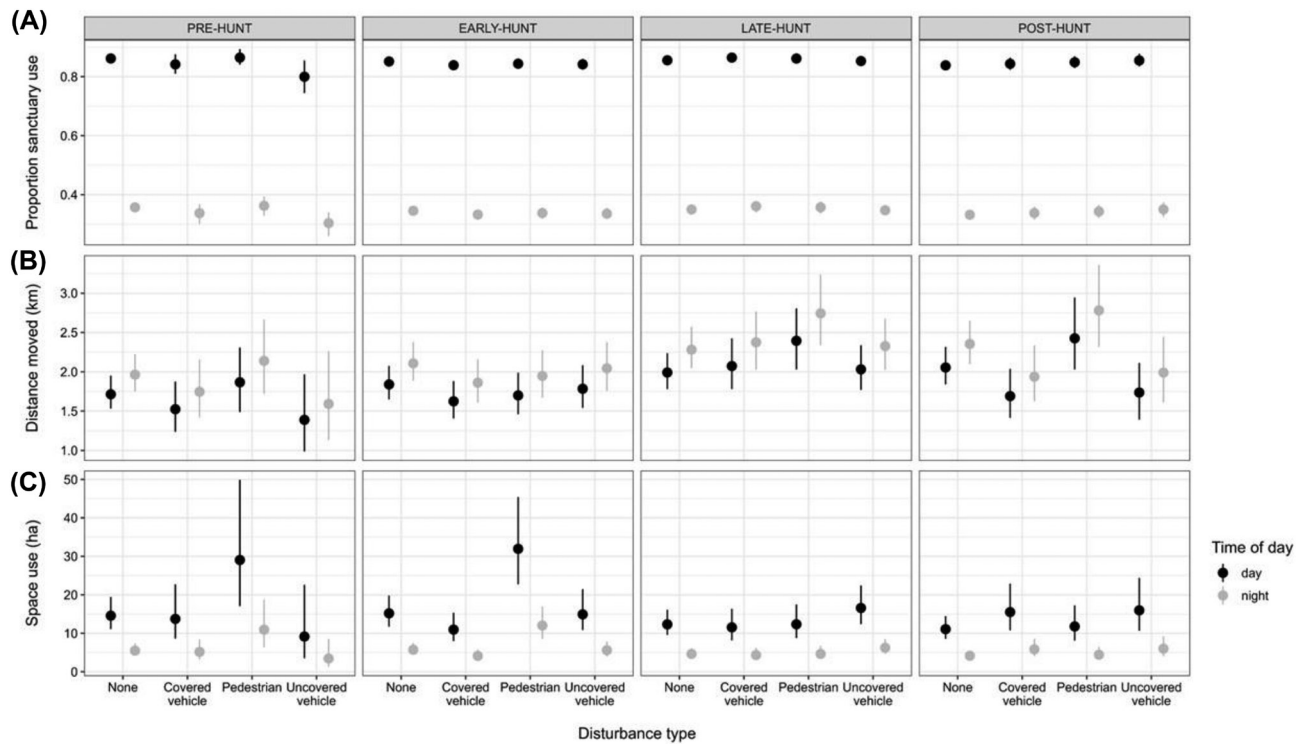


Figure 5. Model-predicted responses of mallards *Anas platyrhynchos* to disturbance on sanctuaries across hunting periods and time of day split by response type: panel (A) proportion sanctuary use; (B) distance moved (km); (C) space use (ha). The 85% credible intervals are shown as vertical bars. Data are from mallards marked with GPS-GSM telemetry in western Tennessee, USA, during 1 November–28 February 2019–2022.

35.0% ( $\beta=0.30$ ,  $SE=0.10$ ) during the late-hunt and 44.8% ( $\beta=0.07$ ,  $SE=0.24$ ) during the post-hunt period relative to undisturbed mallards (Fig. 5C; Supporting information). Lastly, mallards used less space in response to each additional cumulative disturbance. The interaction between cumulative disturbance and hunting season was significant, indicating the space use decreased more rapidly in response to cumulative disturbance during the hunting period (Supporting information). Specifically, space use decreased 12.2% ( $\beta=-0.13$ ,  $SE=0.03$ ) for each additional disturbance encounter during the hunting period and 4.0% ( $\beta=0.09$ ,  $SE=0.04$ ) for each additional disturbance encounter outside the hunting period (Fig. 6C; Supporting information).

## Discussion

Wildlife responses to pulses of anthropogenic disturbances are highly context-dependent and may be constrained in landscapes offering little respite from human threats such as hunting. We document variable and context-dependent changes in mallard movements, space use, and sanctuary fidelity in response to experimental disturbance on waterfowl sanctuaries with limited support for our initial hypotheses. For instance, we expected mallards would exhibit greater sensitivity to human disturbance during the hunting period from broadly ascribing lethal risk to all human activities during

this time. However, mallards were generally more sensitive to our disturbance treatments on sanctuaries outside of the hunting period. Additionally, we predicted mallards would be most sensitive to the uncovered vehicle as we considered it the most threatening stimulus, but mallard responses were inconsistent and suggest greater behavioral changes occurred in response to the pedestrian disturbance (e.g. space use more than doubled during the pre-hunt and early-hunt periods). Further, and contrary to our expectations, mallards rarely abandoned disturbed sanctuaries, particularly during and following the hunting season. This site fidelity despite localized pulses of risk concurs with existing and emerging theory on how animals integrate information about threats across multiple spatial scales (e.g. dynamic landscapes of fear; Sih 2013, Tablado and Jenni 2017, Palmer et al. 2023). Humans and their activities are increasingly recognized as key mediators in dynamic landscapes of fear, and our results suggest that mallards weigh localized, non-lethal risks against surrounding levels of lethal risk when responding to human disturbance (Moleón and Sanchez-Zapata 2023, Palmer et al. 2023). Our findings offer novel insights into the management of anthropogenic disturbances for wintering waterfowl and may serve as an example to other systems impacted by anthropogenic disturbance where wildlife respond to risk from humans by adjusting behavior and using sanctuaries extensively.

Mallards rarely abandoned sanctuaries, further highlighting that animals integrate perceived risk information across

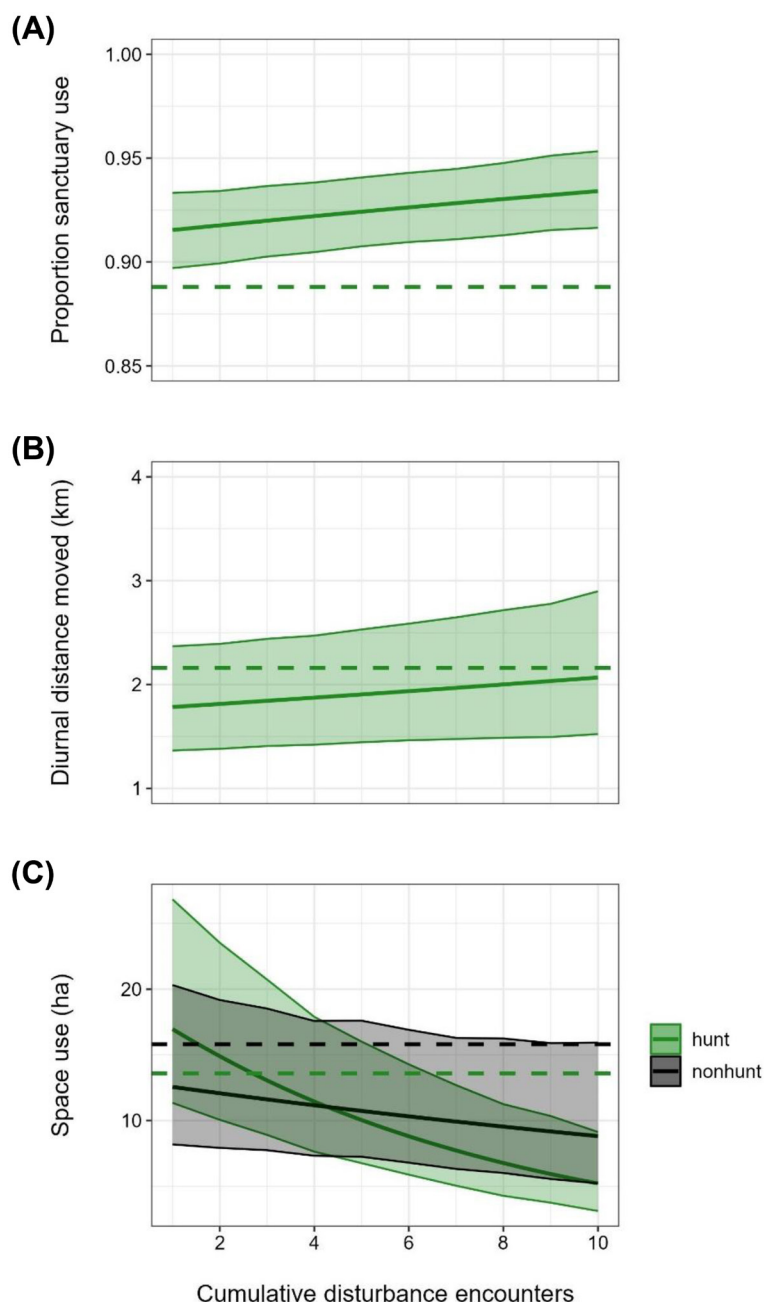


Figure 6. Model-predicted responses of GPS-marked mallards *Anas platyrhynchos* to cumulative disturbance encounters on sanctuaries split by response type: panel (A) diurnal proportion sanctuary use; (B) diurnal distance moved (km); (C) diurnal space use (ha). The 85% credible intervals are shown. The median responses of undisturbed mallards are shown as horizontal dashed lines. The interaction between cumulative disturbance and hunting period was only significant for space use. Data are from mallards in western Tennessee, USA, during 1 November–28 February 2019–2022.

multiple spatial scales within their landscape of fear (Tablado and Jenni 2017, Palmer et al. 2023). Surrounding landscapes offered little respite from risk during hunting season, likely necessitating site fidelity despite localized risk introduced to sanctuaries by disturbance treatments. Moreover, remaining on sanctuaries despite disturbances may therefore reflect a lack of suitable alternative areas rather than habituation (Frid and Dill 2002, Rode et al. 2006, Bejder et al. 2009, Ericsson et al.

2015, Tablado and Jenni 2017). However, sustained sanctuary fidelity after hunting ended may indicate some acclimation to non-lethal disturbances, aided by site familiarity (Rodriguez-Prieto et al. 2014, Gehr et al. 2020), but may also indicate a delayed response to reacclimate to the surrounding landscape of reduced risk from humans (Masto et al. 2024).

The risk–disturbance hypothesis predicts animals will respond more to disturbance stimuli of greater intensity.

Our prediction that mallards would respond more drastically (e.g. move more, use more space) when disturbed with an uncovered vehicle was only partially supported, despite entering wetland units and approaching groups of birds directly. At the hourly-scale, for example, mallards moved > 200% more in response to the uncovered vehicle disturbance on the mornings of disturbance and only decreased sanctuary use in response to the uncovered vehicle disturbance outside of the hunting period. However, the diel-scale results indicate mallards showed more exaggerated responses (e.g. greater diel movements and space use) to the pedestrian disturbance compared to other treatments (Pease et al. 2005). Increased sensitivity to pedestrians, compared to vehicular disturbances, has support in the literature (Papouchis et al. 2001, Ciuti et al. 2012, Westekemper et al. 2018). For instance, Pease et al. (2005) found pedestrians and people on bicycles were more disruptive than vehicles for wintering waterfowl in Virginia, USA. Animals typically react more intensely to pedestrians, perceiving their movements as less predictable (Papouchis et al. 2001, Ciuti et al. 2012, Westekemper et al. 2018). The increased sensitivity to the pedestrian disturbance occurred throughout the nonhunted and hunted periods of our study, suggesting either mallards were unable to distinguish non-lethal pedestrians from actual hunters or that they broadly ascribe risk to pedestrians, a common phenomenon across species (Ciuti et al. 2012, Courbin et al. 2022).

We expected mallards that were disturbed multiple times would habituate and become less sensitive to disturbances (Bejder et al. 2009, Blumstein 2016). However, despite a gradual decrease in space use and increase in sanctuary use as mallards were repeatedly disturbed, as well as reduced movements in response to vehicle disturbances following the hunting period, we caution interpreting these patterns as habituation. We disturbed sanctuaries infrequently (~1/week/sanctuary), and few individuals were disturbed in back-to-back weeks. Thus, long intervals between events may not allow for habituation to disturbances (Rodríguez-Prieto and Fernández-Juricic 2005). Additionally, mallards exposed to multiple disturbances over time experience seasonally dynamic changes in temperature or food availability (Highway 2022), which may impact individual condition or nutritional state and subsequent decision-making and responses to human-induced risk (Gill et al. 2001, Bejder et al. 2009). Moreover, reduced space use could also indicate increased familiarity and higher efficiency in space use over time (Van Moorter et al. 2009). However, following the hunting season, sanctuary use of disturbed mallards did not differ from undisturbed mallards, a response that could indicate some level of habituation to non-lethal disturbances on sanctuaries. In fact, alternative safe wetlands became available because hunting was closed. Perhaps familiarity with sanctuary sites played a part in remaining on sanctuaries following the hunting period, as familiarity should be beneficial for anti-predator behavior (Forrester et al. 2015, Gehr et al. 2020). Moreover, empirical data support that prey animals with imperfect knowledge of predator presence remain in refugia long after the predator departs (Kotler et al. 1992, Sih

1997), which perceptibly could apply to disturbed mallards following the hunting period in our study.

Rather than uniformly amplifying disturbance effects, hunting risk mediated behaviors in a dynamic, context-dependent manner (Tablado and Jenni 2017). For instance, while pedestrian disturbances elicited stronger reactions, vehicle approaches sometimes resulted in decreased movements or space use primarily outside the hunting season. Mallards were initially 'startled' by the vehicle disturbance treatments but ultimately had limited movement thereafter, suggesting some kind of movement compensation or a 'hunkering-down' effect, similar to findings in other studies (Tucker et al. 2018, Doherty et al. 2021, Versluijs et al. 2022). For instance, Suraci et al. (2019) found bobcats *Lynx rufus* reduced diurnal activity by 31% when hearing humans and shifted diel patterns to become more nocturnal. Post-disturbance behavioral shifts like movement reductions potentially mitigated disturbance costs via human avoidance and energy recovery (Riddington et al. 1996, Suraci et al. 2019). While others have shown increased sensitivity to humans at onset of hunting periods (Dooley et al. 2010, Sreekar and Goodale 2015, Courbin et al. 2022), mallards generally were more sensitive during less risky periods, further highlighting the great impact surrounding hunting pressure has on mallard landscapes of fear. Regardless, mallards respond dynamically to disturbance stimuli based on background risk levels, a nuance essential for balancing wildlife conservation and human recreation.

Waterfowl sanctuaries are managed by multiple entities (e.g. US Fish and Wildlife Service, state wildlife agencies, private landowners, private hunt clubs); therefore, the authorized purpose of implementing waterfowl sanctuaries are multi-faceted. However, given multi-use mandates and objectives of many state or federal agencies, pressure to manage both wildlife populations and recreational opportunities is commonplace. Our study indicates that brief and infrequent disturbances on sanctuaries did not shift mallards away from sanctuaries during the hunting season. Therefore, forms of recreation that resemble those of our disturbances (e.g. wildlife viewing and photography, auto tours) could be permitted on a limited basis (~1 h/week), depending on agency goals. However, our results support previous research which found an approximate 30% decline in harvest opportunity when experimental disturbances occurred on waterfowl sanctuaries (Blake-Bradshaw et al. 2023). Here, we documented the mechanism by which harvest opportunity could decline; namely that mallards often 'hunkered down' on disturbed sanctuaries and did not move off sanctuary when disturbed. Thus, other factors such as local harvest opportunity or hunt quality could be impacted and should be considered when determining best management actions. Lastly, our results may also indicate current management practices on sanctuaries such as bi-weekly waterfowl surveys via covered vehicle or infrequent maintenance checks do not scare mallards off of sanctuaries.

Our study highlights the importance of considering the broader landscape context when evaluating wildlife responses to anthropogenic disturbance in protected areas, and



underscores the complex trade-offs experienced by wintering waterfowl. Our study further provides novel information that can be used to inform management decisions related to possible non-consumptive forms of recreation on spatial waterfowl sanctuaries. While mallards appeared resilient to brief disturbances, interspecific differences in responses to anthropogenic disturbance (Pease et al. 2005, Hagy et al. 2017, van der Kolk et al. 2020) suggest that other waterfowl species, particularly those with smaller body sizes, faster life-history (e.g. *Anas carolinensis*) or specialized foraging niches (e.g. *Mareca strepera*) could be more susceptible to negative impacts (Pease et al. 2005, Ackerman et al. 2006, Masto et al. 2022). Importantly, limited behavioral response to anthropogenic disturbance does not necessarily indicate that the disturbance had no effect (Gill et al. 2001, Beale and Monaghan et al. 2004), as individuals exposed to disturbance weigh multiple tradeoffs (e.g. fleeing versus prioritizing energy saving) in deciding whether to or the extent to which they will respond to human-induced risk (Mills et al. 2023). Wildlife also often experience stress or other physiological effects when exposed to humans with subsequent implications for individual condition and fitness (Angelier et al. 2010, Carillet et al. 2020). Thus, future research should investigate species-specific responses to inform targeted conservation strategies and link behavioral responses to individual fitness and population parameters. Additionally, while it was impractical to also disturb mallards located off of sanctuaries given the high sanctuary use documented in our study, future studies should consider comparing mallard responses to disturbances on and off of sanctuaries, especially in systems where sanctuary use is more variable. Mallards exhibited context-dependent behavioral changes while maintaining high site fidelity to sanctuaries, underscoring the need for managers to consider both localized disturbance regimes and regional levels of risk when balancing wildlife protection and recreational opportunities. Moreover, an understanding of mallard responses to brief pulses of anthropogenic disturbance on spatial sanctuaries and the context-dependency of responses can inform the development of broadscale management and conservation approaches to balance population protection with recreational opportunities to ensure healthy, functioning ecosystems.

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## Author contributions

**Abigail G. Blake-Bradshaw:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead); Writing – review and editing (equal). **Nicholas M. Masto:** Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Cory J. Highway:** Conceptualization (equal); Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Allison C. Keever:** Conceptualization (equal); Supervision (supporting); Writing – review and editing (equal). **Jamie C. Feddersen:** Conceptualization (supporting); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Supervision (supporting); Writing – review and editing (equal). **Heath M. Hagy:** Conceptualization (equal); Funding acquisition (supporting); Project administration (supporting); Resources (supporting); Writing – review and editing (equal). **Bradley S. Cohen:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (lead); Project administration (lead); Supervision (lead); Writing – review and editing (equal).

## Transparent peer review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/wlb.3.01340>.

## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.zgmsbccm9> (Blake-Bradshaw et al. 2024).

## Supporting information

The Supporting information associated with this article is available with the online version.

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