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Anthropogenic Disturbance Affects Movement and Increases Concealment in Western Diamondback Rattlesnakes (*Crotalus atrox*)

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ABSTRACT.—**The effects of human disturbance on movements and concealment behavior of Western Diamondback Rattlesnakes (*Crotalus atrox*) were studied at the Arizona–Sonora Desert Museum near Tucson, Arizona. We predicted that *C. atrox* would move more frequently and greater distances, and show higher degrees of concealment in disturbed areas when compared to undisturbed areas. Twenty-five rattlesnakes were equipped with radio-transmitters between July 2005 and September 2011. During the active season, but excluding the mating season, *C. atrox* were less likely to move while in highly disturbed areas than when they were in undisturbed areas. During the mating season, however, *C. atrox* were significantly more likely to move while in highly disturbed areas than when they were in undisturbed areas. During the inactive season, disturbance had no significant effect on the probability of movement. In all seasons, *C. atrox* were more likely to be concealed in highly disturbed areas.**

As the human population increases, human interactions with wildlife increasingly cause direct and indirect disturbance to wildlife. Direct anthropogenic disturbance entails contact between humans and wildlife, and indirect anthropogenic disturbance results from environmental alterations such as construction and settlement (Ohashi et al., 2013). Federal legislations in Canada and the USA already exist to protect species at risk from both direct and indirect human disturbance. Nevertheless, urban sprawl, tourism, and outdoor recreation cause anthropogenic disturbance and pose a threat to global biodiversity (Rodriguez-Prieto and Fernandez-Juricic, 2005). The short- and long-term effects of anthropogenic disturbance must be identified to determine how they influence species persistence.

Human disturbance can alter behavior (Burger, 1994; Ciuti et al., 2012; Ohashi et al., 2013), abundance (Rodriguez-Prieto and Fernandez-Juricic, 2005), habitat selection (Liley and Sutherland, 2007), and reproductive success (Carney and Sydeman, 1999) of vertebrates, including reptiles. Ultimately, human disturbance contributes to reptile endangerment where they become less abundant in disturbed habitats (Brown, 2001). For example, human disturbance reduces the presence of Wall Lizards (*Podarcis muralis*) and Western Whip Snakes (*Hierophis viridiflavus*; Ficetola et al., 2007), promotes avoidance of artificial structures in Timber Rattlesnakes (*Crotalus horridus*; Sealy, 2002), decreases defensive behavior in Cottonmouths (*Agkistrodon piscivorus*; Glaudas, 2004; Glaudas et al., 2006), and alters movement patterns in Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*; Parent and Weatherhead, 2000). Western Diamondback Rattlesnakes (*Crotalus atrox*) may experience higher mortality at urban sites than at undisturbed sites (Nowak et al., 2002). Some rattlesnake populations, however, may be relatively resilient to frequent human disturbances (Brown et al., 2009; Holding et al., 2014).

Seasonality affects movements in rattlesnakes (Waldron et al., 2006). For instance, Timber Rattlesnake movements differ during distinct behaviorally based seasons (foraging, breeding, and hibernation; Waldron et al., 2006). Rattlesnake movements are also a function of the sex and age of the individual (Macartney et al., 1988). In general, males move more often (Waldron et al., 2006) and longer distances than females (Secor, 1994; Waldron et al., 2006; Parker and Anderson, 2007). Additionally, adults tend to move less frequently than juveniles (Secor, 1994). Finally, human disturbance could also potentially affect movement patterns and behavior of rattlesnakes. Frequently disturbed animals use cover to conceal themselves from possible threats (Yarmoloy et al., 1988). For instance, some gravid female rattlesnakes are more concealed in areas that are highly disturbed by humans (Parent and Weatherhead, 2000). Because movement patterns in rattlesnakes depend on season, sex, and age, these effects could mask an effect of anthropogenic disturbance on movement patterns if not accounted for.

We studied the potential effects of anthropogenic disturbance on Western Diamondback Rattlesnakes at the Arizona–Sonora Desert Museum (ASDM) near Tucson, Arizona. Our general hypothesis was that movements and concealment of *C. atrox* are affected by human disturbance. If *C. atrox* are disturbed by anthropogenic activities, then we expected their probability of movement to be higher in areas where there is more anthropogenic disturbance. We also expected that *C. atrox* would be concealed more often in areas of greater anthropogenic disturbance, although if disturbance causes rattlesnakes to move more often, this also may render them concealed less often. To test these predictions, we used movement and concealment data collected via radio-telemetry on 25 *C. atrox* at the ASDM between July 2005 and September 2011. The 40-hectare ASDM features a mostly outdoor experience, including walking paths through various desert habitats and attracts 370,000–400,000 visitors annually. The ASDM is home to five species of rattlesnakes: *C. atrox* (Baird and Girard, 1853), *Crotalus cerastes* (Sidewinder; Hallowell, 1854), *Crotalus molossus* (Black-tailed Rattlesnake; Baird and Girard, 1853), *Crotalus scutulatus* (Mohave Rattlesnake; Kennicott, 1861) and *Crotalus tigris* (Tiger Rattlesnake; Kennicott, 1859); therefore, human-rattlesnake encounters are frequent (Poulin and Ivanyi, pers. obs.).

MATERIALS AND METHODS

Study Site and Study Animals.—The ASDM and adjacent Tucson Mountain Park are located approximately 20 km west of Tucson, Arizona, USA (32°14′N, 111°10′W; Fig. 1) in the Sonoran desert. We captured 15 male and 10 female *C. atrox* between July 2005

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FIG. 1. Arizona–Sonora Desert Museum, in Arizona, USA, the site for studying effects of anthropogenic disturbance on Western Diamondback Rattlesnakes.

and September 2011 opportunistically on ASDM grounds and fitted them with radio-transmitters (13g, SI-2T Holohil Systems Incorporated, Carp, Ontario, Canada). We performed coelomic implant and removal surgeries as outlined by Weatherhead and Blouin-Demers (2004). Once they were released at their capture location, we located the rattlesnakes, on average, twice weekly (0–5 times per week), during daylight hours, with the use of an AVM LA12-Q radio-telemetry receiver and an AVM F172-3FB hand-held directional antenna. We changed the order in which we located the snakes to ensure that a given individual was not always located at the same time of day. Although not exactly reflective of perception by non-human vertebrates, we obtained an index of concealment by recording whether the rattlesnake was visible by the observer at the time of location (0 = concealed, 1 = visible). We mapped all rattlesnake locations with a GPS unit (Garmin 12XL, 1–2 m accuracy).

Spatial Analyses.—We used ArcGIS v. 10.1 (Environmental Systems Research Institute Inc., Redlands, California) for spatial analyses of snake movements. We used Hawth's Tools (Beyer, 2004) to calculate distance (m) moved between subsequent locations. Given the size of the study animals and the accuracy of the GPS, we considered locations <4 m apart to represent no movement. Our study area was defined based on a convex polygon encompassing all rattlesnake locations. We used Google Earth (Google Inc.) to delineate polygons of four disturbance levels within the study area (Table 1). Once we created disturbance polygons in ArcGIS, we used the Buffer Tool to apply 2-, 5-, and 10-m buffers on all disturbance layers, because we reasoned that disturbance affects the neighboring areas. Where polygons overlapped, precedence was given to polygons of the highest disturbance category (Beale, 2014). Analyses based on these three buffering distances produced qualitatively similar results (Beale, 2014). Therefore, we present the results based on only the 5-m buffer.

Statistical Analyses.—All statistical models were built with R software (R Core Team, 2013) and we selected the best models based on Akaike information criterion (AIC; Akaike, 1973). We used logistic regression to analyze the probability of movement and the probability of being visible, and we used linear mixed-effects models to analyze distance moved. Individual ID, sex, and season were included as main effects of interest in all models. We included individual ID as a random effect to account for autocorrelation and interindividual differences in behavior. We also included the effect of sex because movement patterns and behavior may differ between male and female snakes (Blouin-Demers and Weatherhead, 2002). Lastly, we included the effect of season (mating season, active season outside of the mating season, inactive season), because mean distance moved per week varies depending on the season (Fig. 2). *Crotalus atrox* has two

TABLE 1. Criteria for disturbance level classification and the number of snake locations per disturbance level.

Level	Description	Number of snake locations
1	Areas outside Arizona–Sonora Desert Museum (ASDM) grounds and without human structures.	1,230
2	Areas within ASDM grounds not classified as Level 3 or 4, and human establishments outside ASDM grounds.	254
3	Areas of buildings open to staff, dirt paths, bridges, tunnels, and shade areas accessible by a dirt path.	410
4	Areas of buildings open to the public, paved paths, stairs, restrooms, drinking fountains, parking lots, smoking areas, first-aid areas, and shade areas accessible by a paved path.	439

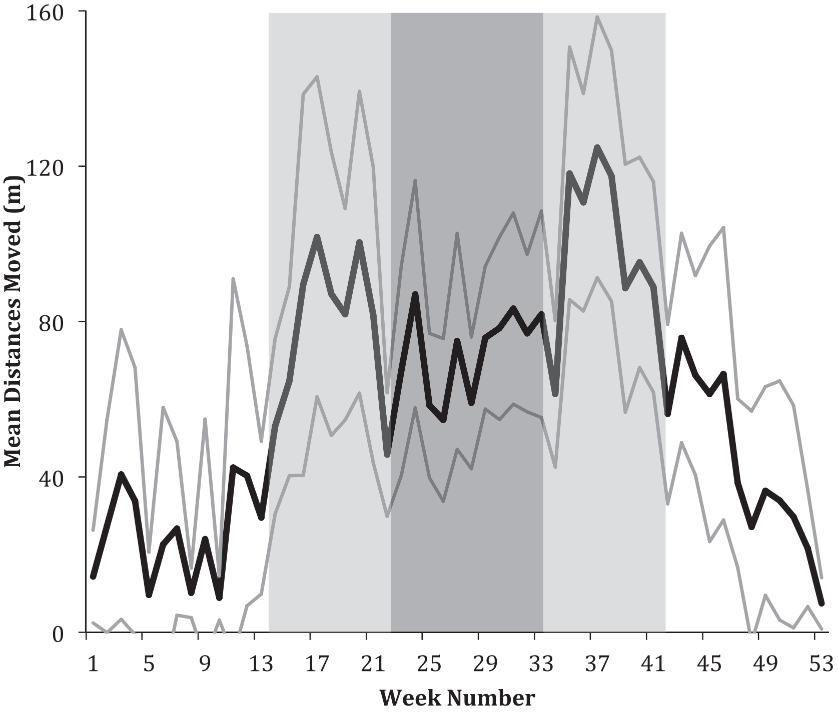

FIG. 2. Mean distance moved (m, dark line) and 95% confidence intervals (CI, pale lines) for each week of the year. Seasons are represented by colored boxes. The inactive season is represented by a white box (20 October–30 March), the two mating seasons are represented by light gray boxes (31 March–25 May; 18 August–19 October), and the active season outside of the mating season is represented by a dark gray box (25 May–17 August).

mating periods per year: one in the spring and one in the fall (Taylor and DeNardo, 2005). We defined the active season outside of the mating season as the period between the spring and fall mating periods. Temperature was not included as an effect because it was collinear with season, and season had better explanatory power in our initial models (Beale, 2014).

RESULTS

We followed the 25 rattlesnakes for periods ranging from 47 to 1,773 days and obtained a total of 2,332 locations (12–272 locations per individual). The probability of human disturbance affecting movement of rattlesnakes varied with season. The best model for the probability of movement as a function of disturbance indicated a significant interaction between season and disturbance (Table 2). Separate analyses, using the model indicated in Table 2, were conducted for each season (Fig. 3). During the mating season, rattlesnakes were significantly more likely to move while in highly disturbed areas ($P = 0.03$). Conversely, during the active season outside of the mating season, rattlesnakes were significantly less likely to move while in highly disturbed areas ($P = 0.042$). During the inactive season, disturbance was not a significant predictor of the probability of movement ($P = 0.295$). The best predictive model for the distance moved as a function of disturbance did not

TABLE 2. Model selection and details of the competing model (*) and final averaged model for probability of movement of Western Diamondback Rattlesnakes in areas of varying disturbance levels. *k* = the number of parameters in the model, AIC = Akaike information criterion value, and ΔAIC = difference between AIC values for the best model (**) and each other model. Each model included a random intercept for individual ID, as well as random slopes between both individual ID and season, and individual ID and sex.

Model	*k*	AIC	ΔAIC
Probability of movement = disturbance + sex + season + disturbance × sex + disturbance × season + sex × season + disturbance × sex × season	22	2,427.35	5.87
Probability of movement = disturbance + sex + season + disturbance × sex + disturbance × season + sex × season	20	2,426.55	5.07
Probability of movement = disturbance + sex + season + disturbance × season + sex × season	19	2,425.01	3.53
*Probability of movement = disturbance + sex + season + disturbance × season	17	2,423.28	1.80
**Probability of movement = disturbance + season + disturbance × season	16	2,421.48	0
Coefficient	Value (SE)	DF	*P*
Intercept	2.20 (0.27)	2,292	<0.0001
Disturbance	−0.20 (0.11)	2,292	0.058
Sex	−0.11 (0.24)	2,292	0.645
Season (inactive)	−1.83 (0.29)	2,292	<0.0001
Season (mating)	−0.73 (0.29)	2,292	0.011
Disturbance × season (inactive)	0.25 (0.13)	2,292	0.057
Disturbance × season (mating)	0.45 (0.14)	2,292	0.001

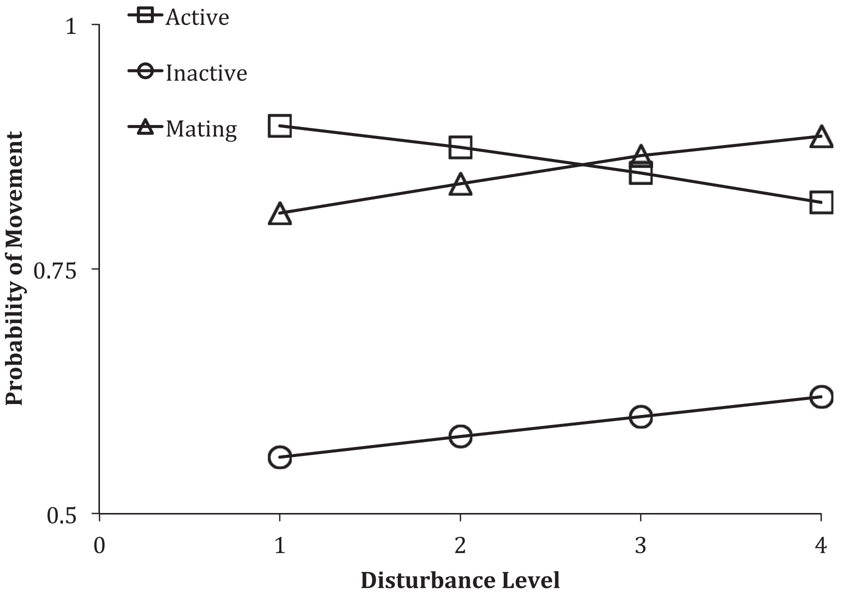

FIG. 3. Probability of movement (0 = no movement, 1 = movement) by Western Diamondback Rattlesnakes near Tucson, Arizona as disturbance increases from level 1 to level 4. Probabilities of movement are plotted separately for the active season outside of the mating season, for the inactive season, and for the mating season.

include disturbance as a predictor variable (Table 3). The best model for the probability of rattlesnake concealment as a function of disturbance (Table 4) indicated that when rattlesnakes were in highly disturbed areas, they were significantly less likely to be visible (or more likely to be concealed; Fig. 4).

DISCUSSION

We modeled the relationships between movement patterns and concealment as a function of anthropogenic disturbance in *C. atrox*, while controlling for several potential confounding variables such as individual, sex, and season. Human disturbance affected the probability of rattlesnake movement and concealment, but human disturbance did not affect the distance moved by rattlesnakes.

We predicted that if *C. atrox* were disturbed by anthropogenic activities, then their probability of movement would be higher in areas where there is more anthropogenic disturbance. In accordance with our prediction, we found that rattlesnakes were more likely to move while in highly disturbed areas than while in undisturbed areas during the mating season (spring and fall). Contrary to our prediction, however, we found that rattlesnakes were less likely to move while in highly disturbed areas when compared to undisturbed areas during the summer active season outside of the mating season. Further, we found that disturbance did not predict the probability of movement during the winter inactive season. The patterns of human visitation at the ASDM may help explain why we found the predicted effect on movement patterns during the mating season only. The spring mating season partially coincides with the period of highest tourist activity at the ASDM (see Beale, 2014 for monthly visitor numbers). As the number of visitors increases in early spring, rattlesnakes are more likely to be disturbed by humans and relocate, which results in more frequent rattlesnake movement. In the summer, however, the ASDM receives very few visitors and,

TABLE 3. Model selection and details of the final model for distance moved (log transformed) of Western Diamondback Rattlesnakes in areas of varying disturbance levels. k = the number of parameters in the model, AIC = Akaike information criterion value, and ΔAIC = difference between AIC values for the best model (**) and each other model. Each model included a random intercept for individual ID, as well as a random slope between individual ID and season.

Model	*k*	AIC	ΔAIC	
Log (distance moved) = disturbance + sex + season + disturbance × sex + disturbance × season + sex × season + disturbance × sex × season	19	5,478.56	32.78	
Log (distance moved) = disturbance + sex + season + disturbance × sex + disturbance × season + sex × season	17	5,470.34	24.56	
Log (distance moved) = disturbance + sex + season + disturbance × sex + sex × season	15	5,459.34	13.56	
Log (distance moved) = disturbance + sex + season + sex × season	14	5,455.07	9.29	
Log (distance moved) = sex + season + sex × season	13	5,449.96	4.18	
Log (distance moved) = sex + season	11	5,450.27	4.49	
**Distance moved = season	10	5,445.78	0	
Coefficient	Value (SE)	DF	*t*	*P*
Intercept	0.12 (0.35)	1,673	41.84	<0.0001
Season (inactive)	−0.71 (0.15)	1,673	−4.64	<0.0001
Season (mating)	0.27 (0.13)	1,673	2.02	0.044

TABLE 4. Model selection and details of the competing model (*) and final averaged model for probability of concealment of Western Diamondback Rattlesnakes in areas of varying disturbance levels. *k* = the number of parameters in the model, AIC = Akaike information criterion value, and ΔAIC = difference between AIC values for the best model (**) and each other model. Each model included a random intercept for individual ID, as well as random slopes between both individual ID and season, and individual ID and sex.

Model	*k*	AIC	ΔAIC
Probability of movement = disturbance + sex + season + disturbance × sex + disturbance × season + sex × season + disturbance × sex × season	22	2,418.99	11.70
Probability of movement = disturbance + sex + season + disturbance × sex + disturbance × season + sex × season	20	2,416.38	9.09
Probability of movement = disturbance + sex + season + disturbance × sex + sex × season	18	2,413.31	6.02
Probability of movement = disturbance + sex + season + disturbance × sex	16	2,410.97	3.68
*Probability of movement = disturbance + sex + season	15	2,409.25	1.96
**Probability of movement = disturbance + season	14	2,407.29	0
Coefficient	Value (SE)	DF	*P*
Intercept	−0.16 (0.18)	2,235	0.292
Disturbance	−0.24 (0.05)	2,235	<0.0001
Sex	0.04 (0.28)	2,235	0.862
Season (inactive)	−1.93 (0.25)	2,235	<0.0001
Season (mating)	−0.04 (0.15)	2,235	0.678

therefore, direct human disturbance to rattlesnakes is much less likely. During winter, rattlesnakes are largely inactive, so direct human disturbance may have less of an impact on their movements. Addressing the separate effects of direct versus indirect human disturbance on wildlife is challenging, because they are usually confounded (Liley and Sutherland, 2007), as was the case in our study, but direct human disturbance must largely be dictated by the number of visitors. Finally, we found no evidence that distances moved by rattlesnakes varied as a function of the level of human disturbance. Therefore, it appears that human disturbance impacts whether a rattlesnake will move, but human disturbance does not appear to impact how far the rattlesnake will move. Overall, therefore, we found mixed support for our hypothesis that movement patterns are dictated by anthropogenic disturbance.

In accordance with our predictions, we found that rattlesnakes were more likely to be concealed while in highly disturbed areas, regardless of season. When visitors are numerous on ASDM grounds, *C. atrox* likely use habitat cover to hide and avoid potentially risky interactions with visitors, as observed in other animal species (Yarmoloy et al., 1988).

Other uncontrolled factors vary between undisturbed and disturbed areas at the ASDM, and these confounding variables also may affect rattlesnake movement patterns. For instance, water availability likely differed between disturbed and undisturbed areas because of plant irrigation on ASDM grounds. Increased water availability could potentially increase plant cover and plant productivity, which in turn could increase prey abundance in the disturbed areas. The abundance of prey and the availability of plant cover both are likely to influence rattlesnake movement patterns and concealment behavior.

Our findings could be used to mitigate the effects of anthropogenic disturbance on *C. atrox*. Because we have identified the areas where most disturbance occurs, measures such as temporary trail closures could minimize rattlesnake disturbance. Furthermore, human–reptile interactions are not well studied, and our study provides valuable insight into the potential consequences of these interactions for the reptiles. For instance, if human-induced changes to rattlesnake movements

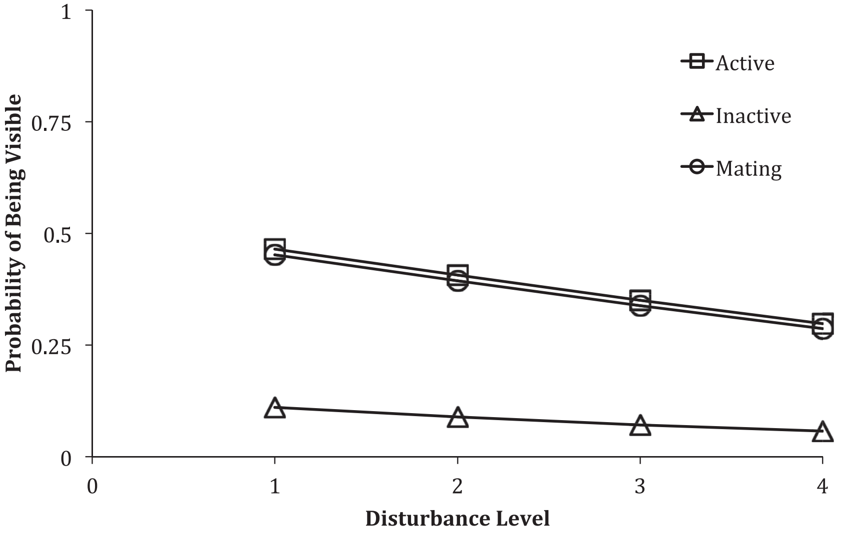

FIG. 4. Probability of Western Diamondback Rattlesnakes near Tucson, Arizona being visible (0 = concealed, 1 = visible) as disturbance increases from level 1 to level 4. Probabilities of being visible are plotted separately for the active season outside of the mating season, for the inactive season, and for the mating season.

and behavior occur, any reduced foraging efficiency could have detrimental effects on rattlesnake populations. Although we were unable to disentangle the effects of direct and indirect anthropogenic disturbance in our observational study, the distinct movement patterns we found when visitor numbers were higher vs. lower suggest that direct human disturbance is a large contributor to the overall effects we documented.

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