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Deer movement and resource selection during Hurricane Irma: implications for extreme climatic events and wildlife

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Extreme climatic events (ECEs) are increasing in frequency and intensity and this necessitates understanding their influence on organisms. Animal behaviour may mitigate the effects of ECEs, but field studies are rare because ECEs are infrequent and unpredictable. Hurricane Irma made landfall in southwestern Florida where we were monitoring white-tailed deer (*Odocoileus virginianus seminolus*) with GPS collars. We report on an opportunistic case study of behavioural responses exhibited by a large mammal during an ECE, mitigation strategies for reducing the severity of the ECE effects, and the demographic effect of the ECE based on known-fate of individual animals. Deer altered resource selection by selecting higher elevation pine and hardwood forests and avoiding marshes. Most deer left their home ranges during Hurricane Irma, and the probability of leaving was inversely related to home range area. Movement rates increased the day of the storm, and no mortality was attributed to Hurricane Irma. We suggest deer mobility and refuge habitat allowed deer to behaviourally mitigate the negative effects of the storm, and ultimately, aid in survival. Our work contributes to the small but growing body of literature linking behavioural responses exhibited during ECEs to survival, which cumulatively will provide insight for predictions of a species resilience to ECEs and improve our understanding of how behavioural traits offset the negative impacts of global climate change.

1. Introduction

A longstanding goal in ecology is to understand the mechanisms that link abiotic factors to organisms and populations. Associated with global climate change, there has been a rapid increase in frequency of extreme climatic events (ECEs). ECEs are weather events that alter ecosystem structure or function outside of the bounds of typical stochasticity [1]. Increased frequency of ECEs has fostered interest in their wide-ranging impacts on ecosystems [1–6]. ECEs have been shown to cause rapid mortality in populations [7–10], broad-scale and enduring alterations in ecosystem function and community structure [11–14], and shifts in ecological community boundaries [15]. The negative consequences of ECEs necessitate a need to understand mechanisms behind resiliency in ecological systems.

Populations can exhibit resiliency to ECEs given favourable habitat heterogeneity over longer time-scales [16–19], but relatively less is understood regarding movement and habitat selection during the event. Studies examining mitigation tactics in regards to ECEs are needed to aid in understanding and predicting how organisms respond to global climate change [20,21]. However, because of their unpredictable nature, quantifying such mitigation tactics is logistically difficult and often opportunistic, given that ECEs cannot be planned for in the study design phase or easily replicated. However, determining which behaviours have the capacity to mitigate negative impacts allows for the quantification of survival mechanisms. Improving our understanding of survival mechanisms allows for more precise predictions regarding vulnerability and persistence for populations in ecosystems where ECEs are predicted to increase [20,21]. Given the limited research regarding behavioural mitigation, such strategies are probably ignored in ecosystem-level climate change assessments.

A limited number of studies have examined alterations in movement patterns during ECEs, which have highlighted mechanisms promoting resilience [22–24]. However, examples are limited to smaller-bodied organisms and are often unintentionally conducted and lack replication because ECEs are unpredictable [22–27]. Further, most studies examining species responses to ECEs are often over longer time-scales and fail to identify the behavioural mitigation strategies which impact survival during ECEs. Given the unpredictability of such events, reporting opportunistic observations, especially observations during ECEs, are valuable because they highlight mechanisms that promote resilience and add to the body of knowledge in regards to species-specific resilience to ECEs, and more broadly climate change.

The range of behavioural responses to ECEs is predicated on phenotypic plasticity. In systems that experience recurrent disturbances (e.g. fire return intervals, hydrological cycles), animals are predicted to have phenotypic adaptations to such disturbances as doing so improves fitness [28,29]. For instance, ephemeral wetland breeders, *Bufo americanus* tadpoles, displayed greater plasticity in metamorphosis timing than a permanent wetland breeder, *Rana utriculari* [30]. Further, in systems where environmental variability is high, behavioural plasticity is expected to be greater [31,32]. For example, post-fire succession has shown to have a 'magnet effect' for some herbivores such that they alter movement behaviour [33–37] and crepuscular, seasonal and successional habitat-use patterns [33,35,38–41] to take advantage of high-quality forage promoted by recurrent fire regimes. Thus, animals that evolve in systems with recurrent disturbances are predicted to have greater behavioural plasticity and therefore may have greater resiliency to ECEs [42,43].

The intensity of disturbance (e.g. wind speed) associated ECEs, and the relative protection provided to an animal in a patch can vary across landscapes, resulting in heterogeneity in severity of ECEs [44–46]. Animal distributions relative to spatial variation in severity can influence the effects of ECEs on populations [44–46]. Combining information regarding habitat heterogeneity, ECE refuge habitat, and habitat use by organisms during an ECE allows for more accurate quantification of the population-level impacts of ECEs. For instance, if habitat use was greater in a habitat type that provided refuge from an ECE, negative effects on populations would be less than if individuals were randomly distributed. Mobile species may modify their distributions relative to severity by moving to refugia [24]. However, few studies have investigated survival and habitat selection during an ECE.

The frequency of hurricanes has increased as a function of intensifying Atlantic warming [47]. Florida sustains more hurricanes than any other state in the USA [48], and experiences numerous tropical storms annually [49]. Distinct wet and dry seasons characterize the Big Cypress Basin physiographical region of southwestern Florida, with 60% of rainfall occurring between May and October, leading to seasonal inundation [49]. Relative to white-tailed deer (*Odocoileus virginianus*) populations in other parts of their range, white-tailed deer (*O.v. seminolus*, hereafter deer) in southwestern Florida occur in lower densities and exhibit lower birth rates, smaller body size, and unique adaptations owing in-part to poor quality soils and seasonal flooding [50–54]. Previous studies have documented deer survival during hurricanes and hypothesized behavioural mechanisms that promote survival (e.g. seeking open prairies free from falling trees, treading water until surge passes) but no behavioural data were collected during the storm [55,56].

Hurricane Irma made landfall on 10 September 2017 where we were remotely monitoring deer using GPS-telemetry. Fine-scale spatio-temporal GPS data allowed us to assess deer survival and behaviour during one of the strongest hurricanes on record in the Atlantic basin [57]. Few studies examining animal's responses to ECEs have documented individuals surviving ECEs [22,24,55,56,58]; however, in most cases, the mechanisms governing survival remain mostly unknown [22]. Spatial variation of an ECE's influence within a landscape may allow mobile species to mitigate the effects of an ECE if they can access areas of lower ECE severity [22]. We report on an opportunistic observation of deer impacted by Hurricane Irma to provide a unique case study of the behavioural response of a large mammal during an ECE, mitigation strategies for reducing the severity of the ECE effects and the demographic effect of the ECE based on known-fate of individual animals. Our work contributes to the small but growing body of literature linking behavioural responses to ECEs to survival, which cumulatively will provide insight for predictions of a species' resilience to ECEs and climate change.

2. Methods

Our study area included Florida Panther National Wildlife Refuge (FPNWR) and the northern units of Big Cypress National Preserve (BCNP) in the Big Cypress Basin physiographical region of southwestern Florida. This area experiences distinct wet and dry seasons and topography is characterized by minimal relief with slight ridges delineating relatively flat basins interspersed with depressions that can retain standing water throughout the dry season. During 2015–2017, we captured deer via net-gunning from helicopters, rocket netting and chemical immobilization via darting following the methods outlined in Cherry *et al*. [37] and protocols accepted by the University of Georgia IACUC permit A2014 07-009-Y3-A1. During the 2015–2017 capture seasons, we collared 263 deer with Iridium ATS (Advanced Telemetry Systems, Isanti, MN) Model G2110E GPS collars programmed to record a location every 3–4 h on a rotating schedule such that each hour of the day was represented every 4 days, of which 59 deer were equipped with functioning collars (19 males, 40 females) during Hurricane Irma.

Hurricane Irma made landfall in southwestern Florida on Marco Island at 15.30 eastern standard time (EST) 10 September 2017, as a category 3 hurricane with maximum sustained winds of 180 km h^{-1} and gusts of 228 km h^{-1} [57]. The eye of the storm tracked east of Naples and Fort Myers, approximately 21–82 km west of the study area at 20.00 EST as a category 2 hurricane [57]. While the hurricane weakened as it made landfall, the wind field of the hurricane expanded significantly, with winds extending 668 km from the eye [57]. Hydrological wells recorded increased water levels between 0.27 and 0.30 m from 9 to 10 September (FPNWR, M. Danaher 2017, unpublished data) and Hurricane Irma caused extensive flooding of low lying areas [59].

We derived habitat data from Florida Natural Areas Inventory Cooperative Land Cover data (CLC, 10 m resolution, [60]). We reclassified habitat data into 10 cover types using CLC, v. 3.2 site-level land cover data (electronic supplementary material, appendix SA1: table S1), six of which were included in this analysis: pine forest, hardwood swamp, marsh, prairie, shrub and hardwood hammock. Once cover types were reclassified, we calculated Euclidian distance to each cover type from each raster cell to provide a continuous distance surface for each land cover type. We used a digital elevation model as elevation data (30 m resolution, [61]).

To assess the effects of Hurricane Irma on resource selection, we fit a step-selection function and used conditional logistic regression to estimate relative probability of selection (SSF; [62,63]). SSFs address issues associated with the definition of available habitat associated with resource selection functions by using a case–control design at the step level [62]. Within an SSF framework, availability is characterized by two components, step length and turn angle [64]. Turn angles are measured as the angular change in bearing relative to the bearing of the previous step resulting in values ranging from $-\pi$ to π, and step length is the straight-line distance between sequential GPS locations. Availability is defined by the movement process such that SSFs constructs 'available' steps from observed distributions of step length and turn angles from each observed location. Using GPS locations collected during the wet season and during the hurricane, which we defined as 1 May–11 September 2017, we drew relative turn angles and step distances from observed data for all individuals, except the focal animal, to reduce problems of potential circularity [63]. We compared 15 'available' locations at each 'used' GPS location.

To examine how Hurricane Irma altered habitat selection, we created conditional logit models. Conditional logit models are similar to standard logistic regression but require that the 'used' steps be compared to the number of 'available' steps, thus all steps were assigned a 'step identifier', which served as our stratum variable. We used the unique deer identification number as a cluster variable to account for individual variation in movement patterns which have the potential to bias population-level selection coefficients [62,65]. We used a variety of remotely sensed data and a categorical variable to represent the day of the storm in our conditional logit models. We extracted elevation and Euclidian distance to each cover type for each 'used' and 'available' deer location. We created a categorical variable to represent the day of Hurricane Irma; we assigned GPS locations taken on the day of Irma (10 September 2017) a categorical 'day of storm' and all other GPS locations during the wet season (1 May–9 September 2017) 'normal'. We scaled and centred all variables used in our models and no explanatory variables used exhibited high correlation ($|r| > 0.7$). We developed candidate models using various combinations of distance to land cover type, and elevation and interacted all these variables with the 'day of storm' (electronic supplementary material, appendix SA1: table S2). We used Akaike's information criterion (AIC) to identify a top model from the set of candidate models [66]. Models were fitted using the survival package [67] in v. 3.5.1 of program R [68].

To examine excursion events from each animal's home range during Hurricane Irma, we calculated each deer's seasonal 95% occurrence distribution [69] using continuous time movement models ([70], hereafter seasonal home ranges). Seasonal home ranges were estimated for each animal during the pre-storm wet season, 1 May–9 September 2017, using package ctmm [71] in v. 3.5.1 of program R [68]. We calculated the Euclidean distance from the seasonal home range boundary to animal locations recorded on the day of Hurricane Irma.

We assessed factors associated with excursion events from an animal's seasonal home range during the storm by fitting a candidate set of logistic regression models to predict the probability of an animal leaving their seasonal home range using the package lme4 [72]. Candidate models reflected all possible linear and additive combinations of variables that we hypothesized may influence the probability of an animal exhibiting excursive behaviour (e.g. sex, seasonal home range area, maximum elevation within the seasonal home range and proportion of seasonal home range within pine forests). No explanatory variables used exhibited high correlation ($|r| > 0.7$). We used AIC to identify a top model from the set of candidate models [66]. We assessed goodness-of-fit using the Hosmer–Lemeshow test [73].

We calculated movement rates ($m\ h^{-1}$) for each deer using relocation data collected every 3–4 h for 7 days before and after Hurricane Irma. We assigned GPS locations a storm status, 'day of storm' if the location was taken on 10 September 2017 and 'normal' if the location was taken two weeks before and after the storm (3–9 September 2017 and 11–17 September 2017, respectively). We fitted linear mixed effects models to predict movement rate as a function of direct and interactive effects of sex and storm status (i.e. day of storm, normal) while treating the animal-specific intercepts as random effects. We used the Satterthwaite method to approximate the degrees of freedom and computed p-values for direct effects and interactions using t-statistics. All analyses were conducted in v. 0 3.5.1 of program R [68].

3. Results

During the wet season prior to Hurricane Irma (1 May–9 September 2017), we recorded 137 120 GPS locations from 59 deer (34 988 males; 102 132 females) with functioning GPS collars (19 males, 40 females), and on the day of Hurricane Irma (10 September 2017), we recorded 324 GPS locations (98 male, 226 female). Deer modified habitat selection during Hurricane Irma (figure 1*a*). During the wet season, most deer locations were in marshes, hardwood swamps, prairies and pine forest, but during Hurricane Irma, most were located in pine forests (electronic supplementary material, appendix SA1: table S3). During Hurricane Irma, deer increased selection of pine forests ($\beta = -0.97$, s.e. ± 0.31, $p < 0.001$), hardwood swamps ($\beta = -0.43$, s.e. ± 0.24, $p = 0.04$) and higher elevations ($\beta = 0.43$, s.e. ± 0.14, $p = 0.03$), and increased avoidance of freshwater marshes ($\beta = 0.86$, s.e. ± 0.25, $p = 0.003$) and shrub habitat ($\beta = 1.39$, s.e. ± 0.43, $p > 0.001$, figure 2; electronic supplementary material, appendix SA1: table S5).

Average seasonal home range area for all deer was 2.01 km^2 (s.e. $\pm 0.24\ km^2$; 1.01 km^2, s.e. $\pm 0.09\ km^2$ females; 4.12 km^2, s.e. $\pm 0.43\ km^2$ males). During Hurricane Irma, 53% of deer (63% of females; 32% of males) embarked upon excursions an average of 193 (s.e. $\pm$ 50.11) m from their seasonal home range (electronic supplementary material, appendix SA1: table S6). The top model (electronic supplementary material, appendix SA1: table S7) indicated that the probability that deer left their seasonal home range decreased with seasonal home range area ($\beta = -0.86$, s.e. $\pm$ 0.36, $p = 0.02$, figure 1*b*). The Hosmer–Lemeshow test indicated the top model fit the data well ($\chi^2 = 11.5$, $p = 0.17$). Seven days before, the day of, and seven days after Hurricane Irma, movement rates for females were 49 (s.e. $\pm$ 4.32), 73 (s.e. $\pm$ 8.44) and 47 (s.e. $\pm$ 8.83) $m\ h^{-1}$, respectively; for males, movement rates were 89 (s.e. $\pm$ 12.2), 67 (s.e. $\pm$ 12.8) and 55 (s.e. $\pm$ 10.6) $m\ h^{-1}$, respectively (figure 1*c*). The day of Hurricane Irma, deer movement rates were significantly higher ($\beta = 0.31$, s.e. ± 0.10, $p = 0.002$; electronic supplementary material, appendix SA1: table S8), and there were sex-specific

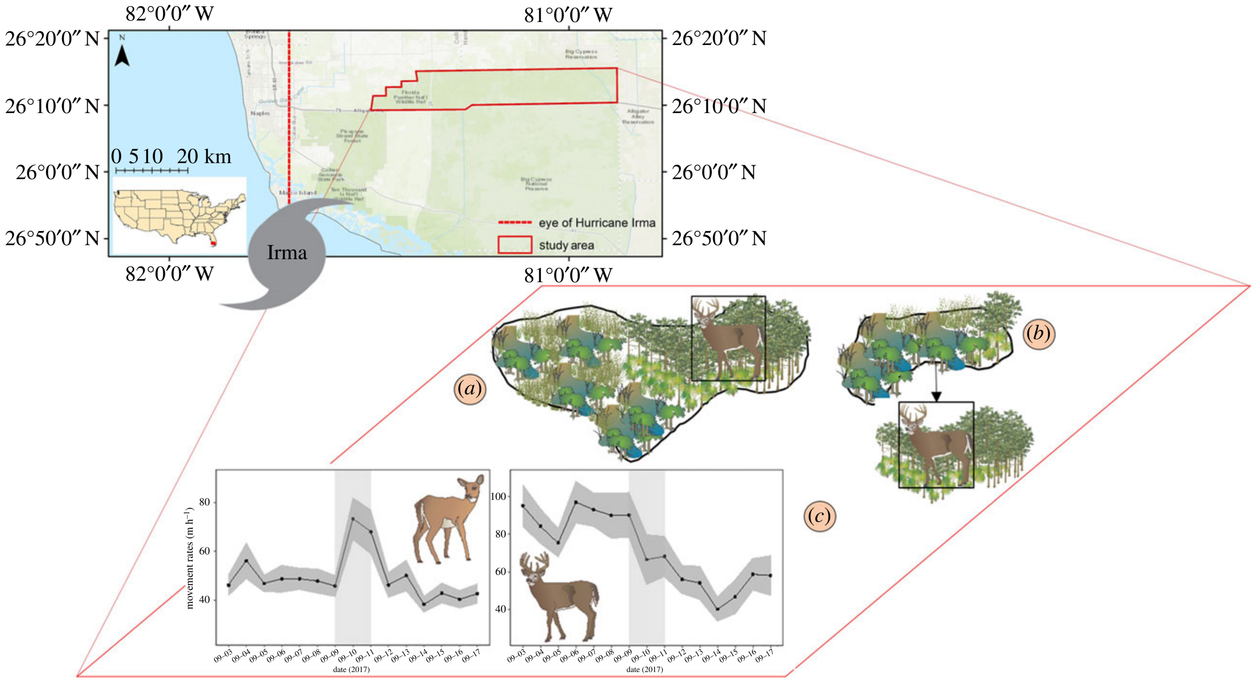

Figure 1. Overview of major findings for white-tailed deer in FPNWR and BCNP in regards to Hurricane Irma. (*a*) Deer selected higher elevations and pine forests in a higher proportion than they were available across the landscape. (*b*) More than half of the deer being monitored left their seasonal home range, and this was related to home range area such that individuals with smaller home ranges were more likely to leave their home range. (*c*) Movement rates (m h^{-1}) for female (left) and male (right) deer 7 days before, the day of, and 7 days following Hurricane Irma (3–9, 10 and 11–17 September 2017, respectively). Highlighted in light grey is the day of Hurricane Irma. Dark grey represents standard error around the average movement rates. (Online version in colour.)

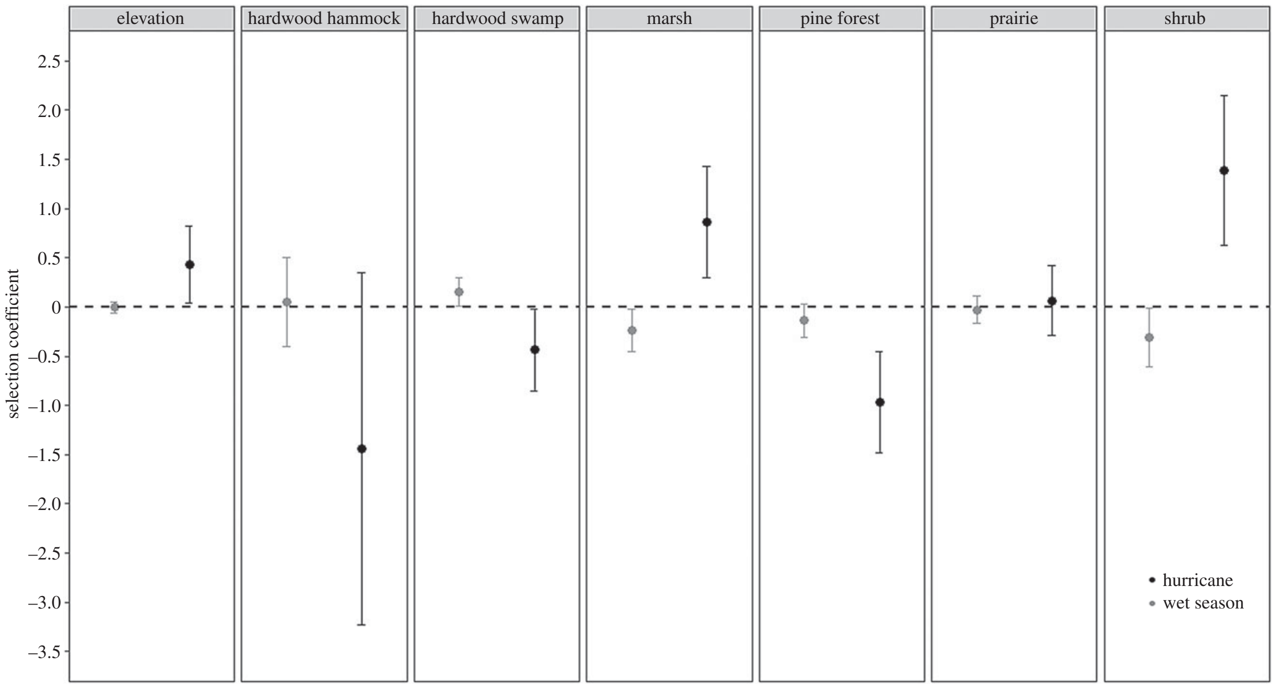

Figure 2. Wet season- and Irma-specific selection coefficients for all white-tailed deer during Hurricane Irma ($n = 59$) with respect to elevation and distance to habitat type. Excluding elevation, negative values indicate selection for a habitat, and positive values indicate avoidance. Error bars indicate 95% confidence intervals, and the dotted line indicates no selection. Data were collected between 1 May 2017 and 11 September 2017.

differences in movement rates ($\beta = 0.43$, s.e. ± 0.14, $p = 0.004$, figure 1*c*; electronic supplementary material, appendix SA1: table S8). No deer died during or within 72 h of the storm.

4. Discussion

ECEs are predicted to increase in strength and frequency [1,6]. Our work addresses a need for studies that link behaviour and survival of organisms during ECEs [20,22,74]. Such work will improve our understanding of how behavioural traits mitigate the negative effects of ECEs on ecosystem population dynamics. Our study documents temporal space-use patterns by a large mammal during an ECE and informs how highly mobile species may respond to such an event in a heterogeneous landscape, and ultimately, provide insights on the mechanisms driving survival.

To mitigate the effects of the storm, deer increased movement rates and moved to higher elevations and areas of dense forested vegetation (i.e. pine forests and hardwood swamps), often leaving their home range to seek such areas. Contrary to our findings, others have suggested deer survival during hurricanes is attributed to forest avoidance [55] as there is evidence that hurricanes cause considerable damage to forested areas in south Florida [55,75,76]. However, forest damage as a result of a hurricane (e.g. fallen and snapped trees) is more a function of canopy composition, structure, and age as opposed to wind speeds [77]. If forested areas had favourable structure and composition which minimizes significant hurricane damage, such areas should buffer the negative impacts associated with hurricane force winds. Wind speed and mixing dynamics differ relative to vertical structure of vegetation such that wind speeds are typically lower at the mid-story or ground level (2 m off ground, [78]). Thus, animals in forested areas can experience wind loads as low as one half of those experienced by animals in open environments [79], suggesting forests should offer relatively more protection from hurricane force winds than open areas. Given the strong selection by deer for forested habitat, it is probable that forests were safer owing to lower wind speeds and less flooding compared to the surrounding open environments (e.g. marshes and prairies). Moreover, while overall deer selected for higher elevations (less flooding), the wind protection provided by hardwood swamps probably offset the flooding such areas likely experienced.

We detected an effect of sex on movement rates, which probably stems from the timing of the storm relative to reproductive chronology. Hurricane Irma made landfall shortly after the breeding season, which typically peaks around August in south Florida [80]. During the breeding season, males dramatically increase movement rates, and rates decline thereafter [81,82], thus the increased movement rates by males prior to the storm were probably driven by breeding season behaviour. Despite differences in movement rates before and after Hurricane Irma, we found that movement rates increased drastically on the day of the storm, and that male and female movement rates were most similar during the storm. This trend is probably associated with seeking protection from the storm (i.e. high winds and flooding), as evidenced by the numerous seasonal home range excursions and the selection of forested areas. Over half of the deer we were monitoring temporarily left their seasonal home range, and deer with smaller seasonal home ranges were more likely to leave those areas. The probability of an animal having refuge habitat (forested areas with higher elevation) decreased with home range size, so it is likely seasonal home range area is a proxy for the amount of refuge habitat available to a given deer during Hurricane Irma. Generally, excursions from a home range are associated with increased predation risk because of a lack of familiarity with the area [83]. This may be particularly true in our study as most deer that embarked upon excursions moved to pine forests and hardwood swamps, areas associated with Florida panthers [84,85]. However, it is possible that predation risk decreased temporarily owing to storm conditions [86], or the risk imposed by the storm simply outweighed the risk of predation.

Others have demonstrated changes in habitat use by animals as a result of ECEs [22,24,87], and our results corroborate previously described mechanisms governing survival [22,87]. While it is likely most terrestrial animals increase survival during storms and flooding by seeking refuge [88], the habitat features or composition needed to survive in these areas are rarely studied. Deer are highly mobile, and during Hurricane Irma, deer had access to refugia, which was probably driven by the variation in vegetation structure across habitat patches. Mobility of deer and the spatial heterogeneity in storm severity resulting from variation in vegetation were probably important drivers of survival during Hurricane Irma. Thus, in landscapes where the severity of ECEs varies by patch type, an animal's mobility and access to refuge sites may be important predictors of their ability to mitigate the effects of ECEs.

Our system experiences recurrent disturbances in the form of wild and prescribed fire and seasonal flooding, and experience tropical storms frequently [89]. Expectedly, deer in this area are noted for their adaptations to the unique environment [50,52,90]. Our results suggest adaptations to hurricanes as all deer monitored survived and selected habitats that probably experienced less flooding and wind severity. However, a broad generalization of ECE's is that animals cannot adapt to such events, given they are infrequent and unpredictable [91]. Thus, behavioural responses to the storm could be an example of an exaptation, which are selective and heritable traits that evolved for a particular purpose which are designated for a new use [92]. However, adaptive responses may also stem from behavioural plasticity that exists in this population owing to recurrent disturbances. Behavioural plasticity is expected to increase with environmental variability [31,32], when dynamic environmental factors induce an adaptive behaviour which improves fitness [20,74,93]. Deer select areas with higher elevation as water levels increase with seasonal flooding [54], and therefore responses observed here may be an extension of traits generalized to deal with storm conditions. When a species-specific response to a recurrent disturbance and an ECE are similar, then adaptive phenotypic plasticity may exist in that system [94]. Thus, similarities between a recurrent disturbance and an ECE may predict species-specific resilience and responses to ECEs.

There is a need for studies that examine how species behaviourally respond to ECEs across many ecological systems. Behavioural adaptations in one system may not occur in other systems, because a tight evolutionary linkage exists between environmental variation and behavioural plasticity, and this linkage drives ecosystem-specific adaptations (e.g. [33,95,96]). For example, deer in systems that do not experience frequent flooding and tropical storms may respond differently to a hurricane than deer in our study. Further, adaptive behavioural plasticity does not predicate upon environmental variation in every system [94] as some species have shown no behavioural modification to recurrent disturbances despite negative fitness consequences [97]. Little is known about terrestrial species responses to the immediate negative effects of hurricanes, but emerging evidence suggests that some adapted behaviours make species more susceptible to the negative impacts [26], while others have demonstrated that animals can detect environmental changes as a result of hurricanes and move to habitats that offset the negative effects [24]. Whether a population's resilience to an ECE is a function of experiencing a recurrent disturbance which has similar characterisics to an ECE is an open and important question.

ECEs have a high probability of inflicting population-level consequences for animals by causing reproductive failure [98,99], direct mortality [100–102] and reduced resource availability [54,58]. Given ECEs are expected to increase [1,2,5,6], there should be an increased emphasis in research examining behavioural mechanisms species employ to offset the negative effects on ecosystems. We report several behaviours employed by a large mammal to mitigate the negative effects of an ECE. Our results highlight the importance of considering exaptations, local adaptations, behavioural plasticity, mobility and access to refugia when predicting their vulnerability to ECEs. Documenting behavioural mechanisms employed by animals to mitigate the effects of ECEs will improve our understanding of how individuals and populations will respond in environments where ECEs are expected to become more common and severe [1,2,5]. Future work should report outcomes of ECEs on ecosystems, and strive to identify the mechanisms that govern the resilience of populations or communities to the effects of ecological change.

Data accessibility. Raw GPS collar data and script used for statistical analyses can be accessed via the Dryad Digital Repository: https://doi.org/10.5061/dryad.f1vhhmgsk [103].

Authors' contributions. E.P.G., M.J.C., R.B.C., M.L.C. and K.V.M. were fundamental in designing and implementing the telemetry study of south Florida deer; D.A.C. was fundamental in deer capture and data collection in the field as well as some statistical modelling; M.J.C. and R.B.C. helped develop statistical methods and modelling for this paper; M.J.C. contributed greatly to the conceptual framework; H.N.A. compiled data, did a substantial amount of statistical modelling, created all figures and wrote several drafts of the manuscript. All authors contributed substantially to revisions.

Competing interests. We declare we have no competing interests.

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