PROCEEDINGS B

royalsocietypublishing.org/journal/rspb

Research



Cite this article: Abernathy HN, Crawford DA, Garrison EP, Chandler RB, Conner ML, Miller KV, Cherry MJ. 2019 Deer movement and resource selection during Hurricane Irma: implications for extreme climatic events and wildlife. *Proc. R. Soc. B* **286**: 20192230. http://dx.doi.org/10.1098/rspb.2019.2230

Received: 24 September 2019 Accepted: 1 November 2019

Subject Category:

Behaviour

Subject Areas: behaviour, ecology

Keywords:

extreme climatic events, white-tailed deer, habitat selection, movement ecology, hurricane, animal behaviour

Author for correspondence:

H. N. Abernathy e-mail: hna8@vt.edu

Electronic supplementary material is available online at https://doi.org/10.6084/m9.figshare. c.4730018.

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

H. N. Abernathy¹, D. A. Crawford^{1,4}, E. P. Garrison², R. B. Chandler³, M. L. Conner⁴, K. V. Miller³ and M. J. Cherry¹

¹Fish and Wildlife Conservation, Virginia Polytechnic Institute and State University, 310 West Campus Drive, Blacksburg, VA 24061, USA

²Florida Fish and Wildlife Conservation Commission, 1105 SW Williston Road, Gainesville, FL 32601, USA
³Warnell School of Forestry and Natural Resources, The University of Georgia, 180 E Green Street, Athens, GA 30602, USA
⁴Jones Center at Ichauway, 3988 Jones Center Drive, Newton, GA 39870, USA

(D) HNA, 0000-0002-4178-9584; DAC, 0000-0001-6754-0560

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 GPStelemetry. 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].

3

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 1a). 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 $(\beta = 0.43, \text{ s.e.} \pm 0.14, p = 0.03)$, and increased avoidance of freshwater marshes (β = 0.86, s.e. ± 0.25, *p* = 0.003) and shrub habitat (β = 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. $\pm 0.24 \text{ km}^2$; 1.01 km^2 , s.e. $\pm 0.09 \text{ km}^2$ females; 4.12 km², s.e. ± 0.43 km² males). During Hurricane Irma, 53% of deer (63% of females; 32% of males) embarked upon excursions an average of 193 (s.e. ± 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 1b). 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. ± 10.6) m h⁻¹, respectively (figure 1*c*). The day of Hurricane Irma, deer movement rates were significantly higher $(\beta = 0.31, \text{ s.e.} \pm 0.10, p = 0.002;$ 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.

5

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.flvhhmgsk [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.

Acknowledgements. We thank the Florida Fish and Wildlife Conservation Commission, the US Fish and Wildlife Service, and the National Parks Service for supporting this research. We thank C. Morea for providing input on the study and M O'leary and F. Goodwin for aviation planning and piloting. Images of deer (figure 2) were provided courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/). We thank the many technicians for data collection.

Disclaimer. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

References

- Smith MD. 2011 An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol.* 99, 656–663. (doi:10.1111/j.1365-2745.2011. 01798.x)
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO. 2000 Climate extremes: observations, modeling, and impacts. *Science* 289, 2068–2074. (doi:10.1126/science.289.5487.2068)
- Jentsch A, Beierkuhnlein C. 2008 Research frontiers in climate change: effects of extreme meteorological events on ecosystems. *C.R. Geosci.* 340, 621–628. (doi:10.1016/j.crte.2008.07.002)
- Jentsch A, Kreyling J, Beierkuhnlein C. 2007 A new generation of climate change experiments: events, not trends. *Front. Ecol. Environ.* 57, 365–374.
- Ummenhofer CC, Meehl GA. 2017 Extreme weather and climate events with ecological relevance: a review. *Phil. Trans. R. Soc. B* 372, 20160135. (doi:10.1098/rstb.2016.0135)
- Dale VH *et al.* 2001 Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. *BioScience* 51, 723–734. (doi:10. 1641/0006-3568(2001)051[0723:CCAFD]2.0.C0;2)
- Breshears DD *et al.* 2005 Regional vegetation die-off in response to global-change-type drought. *Proc. Natl Acad. Sci. USA* **102**, 15 144–15 148. (doi:10. 1073/pnas.0505734102)
- Gitlin AR *et al.* 2006 Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conserv. Biol.* **20**, 1477–1486. (doi:10.1111/j.1523-1739.2006.00424.x)
- Miriti MN, Rodríguez-Buriticá S, Wright SJ, Howe HF. 2007 Episodic death across species of desert shrubs. *Ecology* 88, 32–36. (doi:10.1890/0012-9658(2007)88[32:EDASOD]2.0.C0;2)

- Thibault KM, Brown JH. 2008 Impact of an extreme climatic event on community assembly. *Proc. Natl Acad. Sci. USA* **105**, 3410–3415. (doi:10.1073/pnas. 0712282105)
- MacGillivray C, Grime J, Team TISP. 1995 Testing predictions of the resistance and resilience of vegetation subjected to extreme events. *Funct. Ecol.* 9, 640–649. (doi:10.2307/2390156)
- Haddad NM, Tilman D, Knops JM. 2002 Long-term oscillations in grassland productivity induced by drought. *Ecol. Lett.* 5, 110–120. (doi:10.1046/j. 1461-0248.2002.00293.x)
- Ciais P *et al.* 2005 Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* **437**, 529–533. (doi:10.1038/ nature03972)
- Mueller RC, Scudder CM, Porter ME, Talbot Trotter R, Gehring CA, Whitham TG. 2005 Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *J. Ecol.* **93**, 1085–1093. (doi:10.1111/j.1365-2745.2005.01042.x)
- Allen CD, Breshears DD. 1998 Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proc. Natl Acad. Sci. USA* 95, 14 839–14 842. (doi:10.1073/pnas.95.25.14839)
- Oliver TH, Brereton T, Roy DB. 2013 Population resilience to an extreme drought is influenced by habitat area and fragmentation in the local landscape. *Ecography* 36, 579–586. (doi:10.1111/j. 1600-0587.2012.07665.x)
- Ross BE, Haukos DA, Hagen CA, Pitman JC. 2016 Landscape composition creates a threshold influencing lesser prairie-chicken population resilience to extreme drought. *Glob. Ecol. Conserv.* 6, 179–188. (doi:10.1016/j.gecco.2016.03.003)
- Martínez-Ruiz M, Renton K. 2018 Habitat heterogeneity facilitates resilience of diurnal raptor communities to hurricane disturbance. *For. Ecol. Manage.* 426, 134–144. (doi:10.1016/j.foreco.2017. 08.004)

- Bailey LD, Ens BJ, Both C, Heg D, Oosterbeek K, van de Pol M. 2019 Habitat selection can reduce effects of extreme climatic events in a long-lived shorebird. *J. Anim. Ecol.* 88, 1474–1485. (doi:10.1111/1365-2656.13041)
- Harmon JP, Barton BT. 2013 On their best behavior: how animal behavior can help determine the combined effects of species interactions and climate change. *Ann. N Y Acad. Sci.* **1297**, 139–147. (doi:10.1111/nyas.12192)
- Berger-Tal O, Polak T, Oron A, Lubin Y, Kotler BP, Saltz D. 2011 Integrating animal behavior and conservation biology: a conceptual framework. *Behav. Ecol.* 22, 236–239. (doi:10.1093/beheco/arq224)
- Boucek RE, Heithaus MR, Santos R, Stevens P, Rehage JS. 2017 Can animal habitat use patterns influence their vulnerability to extreme climate events? An estuarine sportfish case study. *Glob. Change Biol.* 23, 4045–4057. (doi:10.1111/gcb.13761)
- Luja VH, Rodríguez-Estrella R. 2010 Are tropical cyclones sources of natural selection? Observations on the abundance and behavior of frogs affected by extreme climatic events in the Baja California Peninsula, Mexico. J. Arid Environ. 74, 1345–1347. (doi:10.1016/j.jaridenv.2010.04.005)
- Udyawer V, Chin A, Knip DM, Simpfendorfer CA, Heupel MR. 2013 Variable response of coastal sharks to severe tropical storms: environmental cues and changes in space use. *Mar. Ecol. Prog. Ser.* 480, 171–183. (doi:10.3354/meps10244)
- Van De Pol M *et al.* 2010 Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *J. Appl. Ecol.* 47, 720–730. (doi:10. 1111/j.1365-2664.2010.01842.x)
- Donihue CM, Herrel A, Fabre A-C, Kamath A, Geneva AJ, Schoener TW, Kolbe JJ, Losos JB. 2018 Hurricane-induced selection on the morphology of an island lizard. *Nature* 560, 88. (doi:10.1038/ s41586-018-0352-3)

7

- Lescroël A, Ballard G, Grémillet D, Authier M, Ainley DG. 2014 Antarctic climate change: extreme events disrupt plastic phenotypic response in Adélie penguins. *PLoS ONE* 9, e85291. (doi:10.1371/ journal.pone.0085291)
- Hughes BS, Cullum AJ, Bennett AF. 2007 An experimental evolutionary study on adaptation to temporally fluctuating pH in *Escherichia coli*. *Physiol. Biochem. Zool.* **80**, 406–421. (doi:10.1086/518353)
- Alto BW, Wasik BR, Morales NM, Turner PE. 2013 Stochastic temperatures impede RNA virus adaptation. *Evol.: Int. J. Org. Evol.* 67, 969–979. (doi:10.1111/evo.12034)
- Newman RA. 1992 Adaptive plasticity in amphibian metamorphosis. *BioScience* 42, 671–678. (doi:10. 2307/1312173)
- Klopfer PH, MacArthur RH. 1960 Niche size and faunal diversity. *Am. Nat.* 94, 293–300. (doi:10. 1086/282130)
- 32. Morse DH. 1982 *Behavioral mechanisms in ecology.* Cambridge, MA: Harvard University Press.
- Klop E, van Goethem J, de longh HH. 2007 Resource selection by grazing herbivores on post-fire regrowth in a West African woodland savanna. *Wildl. Res.* 34, 77–83. (doi:10.1071/WR06052)
- Irwin LL. 1975 Deer-moose relationships on a burn in northeastern Minnesota. J. Wildl. Manage. 39, 653–662. (doi:10.2307/3800223)
- Raynor EJ, Joern A, Briggs JM. 2015 Bison foraging responds to fire frequency in nutritionally heterogeneous grassland. *Ecology* 96, 1586–1597. (doi:10.1890/14-2027.1)
- Pearson SM, Turner MG, Wallace LL, Romme WH. 1995 Winter habitat use by large ungulates following fire in northern Yellowstone National Park. *Ecol. Appl.* 5, 744–755. (doi:10.2307/1941982)
- Cherry MJ, Chandler RB, Garrison EP, Crawford DA, Kelly BD, Shindle DB, Godsea KG, Miller KV, Conner LM. 2018 Wildfire affects space use and movement of white-tailed deer in a tropical pyric landscape. *For. Ecol. Manage.* **409**, 161–169. (doi:10.1016/j. foreco.2017.11.007)
- Moe SR, Wegge P, Kapela EB. 1990 The influence of man-made fires on large wild herbivores in Lake Burungi area in northern Tanzania. *Afr. J. Ecol.* 28, 35–43. (doi:10.1111/j.1365-2028.1990.tb01134.x)
- Murphy BP, Bowman DM. 2007 The interdependence of fire, grass, kangaroos and Australian Aborigines: a case study from central Arnhem Land, northern Australia. J. Biogeogr. 34, 237–250. (doi:10.1111/j.1365-2699.2006.01591.x)
- Sensenig RL, Demment MW, Laca EA. 2010 Allometric scaling predicts preferences for burned patches in a guild of East African grazers. *Ecology* 91, 2898–2907. (doi:10.1890/09-1673.1)
- Spitz DB, Clark DA, Wisdom MJ, Rowland MM, Johnson BK, Long RA, Levi T. 2018 Fire history influences large-herbivore behavior at circadian, seasonal, and successional scales. *Ecol. Appl.* 28, 2082–2091. (doi:10.1002/eap.1797)
- Chevin L-M, Lande R, Mace GM. 2010 Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS*

Biol. **8**, e1000357. (doi:10.1371/journal.pbio. 1000357)

- Lande R. 2014 Evolution of phenotypic plasticity and environmental tolerance of a labile quantitative character in a fluctuating environment. *J. Evol. Biol.* 27, 866–875. (doi:10.1111/jeb.12360)
- Boucek RE, Soula M, Tamayo F, Rehage JS. 2016 A once in 10 year drought alters the magnitude and quality of a floodplain prey subsidy to coastal river fishes. *Can. J. Fish. Aquat. Sci.* **73**, 1672–1678. (doi:10.1139/cjfas-2015-0507)
- Haslem A, Nimmo DG, Radford JQ, Bennett AF. 2015 Landscape properties mediate the homogenization of bird assemblages during climatic extremes. *Ecology* 96, 3165–3174. (doi:10.1890/14-2447.1)
- White PS, Jentsch A. 2001 The search for generality in studies of disturbance and ecosystem dynamics. In *Progress in botany* (eds U Lüttge, FM Cánovas, R Matyssek, H Pretzsch), pp. 399–450. Berlin, Germany: Springer.
- Murakami H, Levin E, Delworth T, Gudgel R, Hsu P-C. 2018 Dominant effect of relative tropical Atlantic warming on major hurricane occurrence. *Science* 362, 794–799. (doi:10.1126/science.aat6711)
- National Climatic Data Center N, NOAA, US Department of Commerce. 1996 NCDC Storm Events Database. Publication: 1996-01-01. Revision: 2013-12-18. See https://www.ncdc.noaa.gov/stormevents/ ftp.jsp (accessed 1 September 2019).
- Duever M, Meeder J, Meeder L, McCollom J. 1994 The climate of south Florida and its role in shaping the Everglades ecosystem. In *Everglades: the ecosystem and its restoration* (ed. WA Park), pp. 225–248. Boca Raton, FL: St Lucie Press.
- Richter AR, Labisky RF. 1985 Reproductive dynamics among disjunct white-tailed deer herds in Florida. J. Wildl. Manage. 49, 964–971. (doi:10.2307/ 3801380)
- Boulay MC. 1992 Mortality and recruitment of white-tailed deer fawns in the wet prairie/tree island habitat of the Everglades. MS thesis, University of Florida, Gainesville, FL, USA.
- Labisky RF, Boulay MC, Miller KE, Sargent Jr RA, Zultowsky JM. 1995 Population ecology of whitetailed deer in Big Cypress National Preserve and Everglades National Park. Final report to National Park Service, Ochopee, FL, USA.
- Fleming M, Schortemeyer J, Ault J. 1994 Distribution, abundance, and demography of whitetailed deer in the Everglades. In Proc. of the Florida Panther Conf., 1–3 November 1994, Ft Myers, FL. Washington, DC: US Fish and Wildlife Service.
- MacDonald-Beyers K, Labisky RF. 2005 Influence of flood water on survival, reproduction, and habitat use of white-tailed deer in the Florida Everglades. *Wetlands* 25, 659–666. (doi:10.1672/0277-5212(2005)025[0659:I0FW0S]2.0.C0;2)
- Labisky RF, Miller KE, Hartless CS. 1999 Effect of Hurricane Andrew on survival and movements of white-tailed deer in the Everglades. *J. Wildl. Manage.* 63, 872–879. (doi:10.2307/3802800)
- 56. Lopez RR, Silvy NJ, Labisky RF, Frank PA. 2003 Hurricane impacts on key deer in the Florida Keys.

J. Wildl. Manage. 67, 280-288. (doi:10.2307/ 3802769)

- Cangialosi JP, Latto AS, Berg R. 2018 National Hurricane Center Tropical Cyclone Report— Hurricane Irma. National Oceanic and Atmospheric Administration-National Hurricane Center.
- Hooper RG, Watson JC, Escano RE. 1990 Hurricane Hugo's initial effects on red-cockaded woodpeckers in the Francis Marion National Forest. *Trans. North Am. Wildl. Nat. Resour. Conf.* 55, 220–224.
- Zhang B, Wdowinski S, Oliver-Cabrera T, Koirala R, Jo M, Osmanoglu B. 2018 Mapping the extent and magnitude of sever flooding induced by Hurricane IRMA with multi-temporal SENTINEL-1 SAR and Insar observations. Int. Arch.e Photogramm. Remote Sens. Spatial Inf. Sci. 42–43, 2237–2244. (doi:10. 5194/isprs-archives-XLII-3-2237-2018)
- Florida Natural Areas Inventory. 2016 Florida Cooperative Land Cover Map, Version 3.2. Tallahassee, Florida. See http://wwwfnaiorg/ LandCovercfm (accessed 1 February 2018).
- NASA/METI/AIST/Japan Spacesystems, and U.S./ Japan ASTER Science Team. 2011 ASTER Global Digital Elevation Model V002. [Global Digital Elevation Model (GDEM) Version 2]. NASA EOSDIS Land Processes DAAC. See https://doi.org/10.5067/ ASTER/ASTGTM.002 (accessed 1 November 2017).
- Fortin D, Beyer HL, Boyce MS, Smith DW, Duchesne T, Mao JS. 2005 Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86, 1320–1330. (doi:10. 1890/04-0953)
- Thurfjell H, Ciuti S, Boyce MS. 2014 Applications of step-selection functions in ecology and conservation. *Mov. Ecol.* 2, 4. (doi:10.1186/2051-3933-2-4)
- 64. Turchin P. 1998 *Quantitative analysis of movement*. Sunderland, MA: Sinauer Associates.
- Prima M-C, Duchesne T, Fortin D. 2017 Robust inference from conditional logistic regression applied to movement and habitat selection analysis. *PLoS ONE* 12, e0169779. (doi:10.1371/journal.pone.0169779)
- 66. Burnham KP, Anderson DR. 2002 *Model selection* and multimodel inference: a practical informationtheoretic approach. New York, NY: Springer.
- 67. Therneau T. 2015 A package for survival analysis in S. version 2.38. See https://CRAN.R-project.org/ package=survival.
- R Core Team. 2017 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See https:// www.R-project.org/.
- Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM. 2016 Estimating where and how animals travel: an optimal framework for path reconstruction from autocorrelated tracking data. *Ecology* **97**, 576–582.
- Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM. 2015 Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96, 1182–1188. (doi:10.1890/14-2010.1)
- 71. Calabrese JM, Fleming CH. 2016 Gurarie E. ctmm: an R package for analyzing animal relocation data

royalsocietypublishing.org/journal/rspb Proc. R. Soc. B 286: 20192230

8

as a continuous-time stochastic process. *Methods Ecol. Evol.* **7**, 1124–1132. (doi:10.1111/2041-210X. 12559)

- Bates D, Maechler M, Bolker B, Walker S. 2014 Ime4: linear mixed-effects models using Eigen and S4. R package version. 1, 1–23. See https://CRAN.Rproject.org/package=lme4.
- 73. Hosmer Jr DW, Lemeshow S, Sturdivant RX. 2013 Applied logistic regression. Hoboken, NJ: John Wiley & Sons.
- Buchholz R, Banusiewicz JD, Burgess S, Crocker-Buta S, Eveland L, Fuller L. 2019 Behavioural research priorities for the study of animal response to climate change. *Anim. Behav.* **150**, 127–137. (doi:10.1016/j.anbehav.2019.02.005)
- Orr DW, Ogden JC. 1992 The impact of Hurricane Andrew on the ecosystems of South Florida. *Conserv. Biol.* 6, 488–490. (doi:10.1046/j.1523-1739.1992.06040488.x)
- Jayantha O, John B, Lewis H, Mark AH. 1999 The natural South Florida system I: climate, geology, and hydrology. *Urban Ecosyst.* 3, 223–244. (doi:10. 1023/A:1009552500448)
- Myers RK, van Lear DH. 1998 Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. *For. Ecol. Manage.* **103**, 265–276. (doi:10.1016/S0378-1127(97)00223-5)
- Boldes U, Scarabino A, Di Leo JM, Colman J, Gravenhorst G. 2003 Characteristics of some organised structures in the turbulent wind above and within a spruce forest from field measurements. J. Wind Eng. Ind. Aerodyn. 91, 1253–1269. (doi:10.1016/S0167-6105(03)00076-X)
- Vickery PJ, Lin J, Skerlj PF, Twisdale Jr LA, Huang K. 2006 HAZUS-MH hurricane model methodology. I: Hurricane hazard, terrain, and wind load modeling. *Nat. Hazards Rev.* 7, 82–93. (doi:10.1061/ (ASCE)1527-6988(2006)7:2(82))
- Garrison E, Gedir J. 2006 Ecology and management of white-tailed deer in Florida, pp. 1–47. Tallahassee, FL: Florida Fish and Wildlife Conservation Commission.
- Crawford DA, Cherry MJ, Kelly BD, Garrison EP, Shindle DB, Conner LM, Chandler RB, Miller KV. 2019 Chronology of reproductive investment determines predation risk aversion in a felid-ungulate system. *Ecol. Evol.* 9, 3264–3275. (doi:10.1002/ ece3.4947)
- 82. Webb SL, Gee KL, Strickland BK, Demarais S, DeYoung RW. 2010 Measuring fine-scale white-

tailed deer movements and environmental influences using GPS collars. *Int. J. Ecol.* **2010**, 1–12. (doi:10.1155/2010/459610)

- Forrester TD, Casady DS, Wittmer HU. 2015 Home sweet home: fitness consequences of site familiarity in female black-tailed deer. *Behav. Ecol. Sociobiol.* 69, 603–612. (doi:10.1007/s00265-014-1871-z)
- Frakes RA, Belden RC, Wood BE, James FE. 2015 Landscape analysis of adult Florida panther habitat. *PLoS ONE* **10**, e0133044. (doi:10.1371/journal.pone. 0133044)
- Onorato DP, Criffield M, Lotz M, Cunningham M, McBride R, Leone EH, Bass Jr OL, Hellgren EC. 2011 Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation. *Anim. Conserv.* 14, 196–205. (doi:10.1111/j.1469-1795.2010.00415.x)
- Cherry MJ, Barton BT. 2017 Effects of wind on predator-prey interactions. *Food Webs* 13, 92–97. (doi:10.1016/j.fooweb.2017.02.005)
- Matich P, Heithaus MR. 2012 Effects of an extreme temperature event on the behavior and age structure of an estuarine top predator, *Carcharhinus leucas. Mar. Ecol. Prog. Ser.* 447, 165–178. (doi:10. 3354/meps09497)
- Nicolai A, Ansart A. 2017 Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. *Conserv. Physiol.* 5, 1–17. (doi:10.1093/ conphys/cox007)
- Gentry RC. 1974 Hurricanes in South Florida. In Environments of South Florida: present and past: Miami Geological Society memoirs 2 (ed. PJ Gleason), pp. 510–519. Gainesville, FL: Sea Grant Extension Program, Florida Cooperative Extension, University of Florida.
- Chandler RB, Engebretsen K, Cherry MJ, Garrison EP, Miller KV. 2018 Estimating recruitment from capture–recapture data by modelling spatiotemporal variation in birth and age-specific survival rates. *Methods Ecol. Evol.* 9, 2115–2130. (doi:10. 1111/2041-210X.13068)
- Lytle DA, Poff NL. 2004 Adaptation to natural flow regimes. *Trends Ecol. Evol.* **19**, 94–100. (doi:10. 1016/j.tree.2003.10.002)
- Gould SJ, Vrba ES. 1982 Exaptation—a missing term in the science of form. *Paleobiology* 8, 4–15. (doi:10.1017/S0094837300004310)
- Komers PE. 1997 Behavioural plasticity in variable environments. *Can. J. Zool.* **75**, 161–169. (doi:10. 1139/z97-023)

- Chevin L-M, Hoffmann AA. 2017 Evolution of phenotypic plasticity in extreme environments. *Phil. Trans. R. Soc. B* **372**, 20160138. (doi:10.1098/rstb. 2016.0138)
- Lashley MA, Chitwood MC, Kays R, Harper CA, DePerno CS, Moorman CE. 2015 Prescribed fire affects female white-tailed deer habitat use during summer lactation. *For. Ecol. Manage.* 348, 220–225. (doi:10.1016/j.foreco.2015.03.041)
- Dalerum F, Boutin S, Dunford JS. 2007 Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. *Can. J. Zool.* 85, 26–32. (doi:10.1139/z06-186)
- Bailey LD, Ens BJ, Both C, Heg D, Oosterbeek K, van de Pol M. 2017 No phenotypic plasticity in nest-site selection in response to extreme flooding events. *Phil. Trans. R. Soc. B* 372, 20160139. (doi:10.1098/ rstb.2016.0139)
- King B, Hicks J, Cornelius J. 1992 Population-changes, breeding cycles and breeding success over six years in a seabird colony at Michaelmas Cay, Queensland. *Emu* 92, 1–10. (doi:10.1071/MU9920001)
- Bolger DT, Patten MA, Bostock DC. 2005 Avian reproductive failure in response to an extreme climatic event. *Oecologia* **142**, 398–406. (doi:10. 1007/s00442-004-1734-9)
- 100. Mallin MA, Posey MH, Shank GC, McIver MR, Ensign SH, Alphin TD. 1999 Hurricane effects on water quality and benthos in the Cape Fear watershed: natural and anthropogenic impacts. *Ecol. Appl.* 9, 350–362. (doi:10.1890/1051-0761(1999)009[0350: HEOWQA]2.0.C0;2)
- 101. Church DR, Bailey LL, Wilbur HM, Kendall WL, Hines JE. 2007 Iteroparity in the variable environment of the salamander *Ambystoma tigrinum. Ecology* **88**, 891–903. (doi:10.1890/ 06-0896)
- 102. Whiterod NS, Zukowski S, Asmus M, Todd CR, Gwinn DC. 2018 Take the long way home: minimal recovery in a K-selected freshwater crayfish impacted by significant population loss. *Ecol. Indic.* 89, 622–630. (doi:10.1016/j.ecolind. 2018.02.042)
- 103. Abernathy HN, Crawford DA, Garrison EP, Chandler RB, Conner ML, Miller KV, Cherry MJ. 2019 Data from: Deer movement and resource selection during Hurricane Irma: implications for extreme climatic events and wildlife. Dryad Digital Repository. (https://doi.org/10.5061/dryad. flvhhmqsk)