

## EFFECTS OF UNGULATE DISTURBANCE AND WEATHER VARIATION ON *PEDIOCACTUS WINKLERI*: INSIGHTS FROM LONG-TERM MONITORING

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**ABSTRACT.**—Population dynamics and effects of large ungulate disturbances on Winkler cactus (*Pediocactus winkleri* K.D. Heil) were documented annually over a 20-year time span at one plot within Capitol Reef National Park, Utah. This cactus species was federally listed as threatened in 1998. The study began in 1995 to gain a better understanding of life history aspects and threats to this species. Data were collected annually in early spring and included diameter, condition, reproductive structures, mortality, recruitment, and disturbance by large ungulates. We used odds ratio and probability model analyses to determine effects of large ungulate trampling and weather on these cacti. During the study, plot population declined by 18%, with trampling of cactus, low precipitation, and cold spring temperatures implicated as causal factors. Precipitation and temperature affected flowering, mortality, and recruitment. Large ungulate disturbances increased mortality and reduced the probability of flowering. These results suggest that large ungulate disturbances and recent climate regimes have had an adverse impact on long-term persistence of this cactus.

**RESUMEN.**—La dinámica de población y los efectos producidos por ungulados grandes en el cactus Winkler (*Pediocactus winkleri* K.D. Heil) han sido anualmente documentados durante un periodo de 20 años en una parcela del Capitol Reef National Park de Utah. En el año 1998, el gobierno federal catalogó esta especie de cactus como amenazada. Fue en el año 1995 cuando se empezó este estudio con la finalidad de obtener un conocimiento más amplio sobre los aspectos relacionados con la vida y amenazas de dicha especie. La información del estudio se ha recolectado anualmente durante los periodos de primavera temprana y los datos incluyen el estado, diámetro, estructuras reproductivas, mortalidad, reclutamiento y las alteraciones producidas por ungulados grandes. Hemos usado proporción de probabilidades y modelos probabilísticos para determinar los efectos producidos a causa del tiempo y el apisonamiento producido por ungulados. Durante del estudio, la población de la parcela observada disminuyó un 18% a causa del apisonamiento, bajas precipitaciones, y bajas temperaturas primaverales. Precipitación y temperatura han afectado la floración, mortalidad, y reclutamiento. De la misma manera, las alteraciones producidas por ungulados grandes han aumentado la mortalidad y reducido la floración. Estos resultados nos sugieren que las alteraciones producidas por ungulados y el reciente régimen climático han tenido un impacto adverso a largo plazo en la persistencia del cactus Winkler.

Most cactus species are long-lived and adapted to surviving in arid and warm environments characterized by low and variable precipitation and warm temperatures (Benson 1982, Godinez-Alvarez et al. 2003). The survival strategies of cacti evolved to enable them to maintain viable populations in harsh habitats and to withstand periods of drought (Hadley 1972, Solbrig and Orians 1977, Godinez-Alvarez et al. 2003). However, recent human activities and current climate changes are increasing the rarity of some cactus species (Federal Register 1979, 2013, Kass 2001, Godinez-Alvarez et al. 2003, Coles et al. 2012, Spector 2013).

One such group of cacti is the genera *Pediocactus*, which comprises 9 species (FNA 1993+). Members of this genus are distributed

across the western United States (Heil and Porter 2003), and 6 are rare and federally listed under the Endangered Species Act (Federal Register 1997, 1998). One of these rare species is Winkler cactus (*Pediocactus winkleri* K.D. Heil), which occurs in low numbers and small, isolated populations. It is a tiny subglobose cactus that typically grows as solitary stems barely extending above ground (Welsh et al. 2003).

The U.S. Fish and Wildlife Service listed Winkler cactus as threatened in 1998 (Federal Register 1998) because of observed threats from collection and habitat disturbances due to mining, recreation, and livestock. Several sources suggest that livestock may negatively affect Winkler cactus (Heil 1984, Neese 1987, Federal Register 1997). Additionally, impacts from rodent and beetle predation have also

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been documented at several localities (Capitol Reef National Park 2014).

Other closely related *Pediocactus* species have contractile roots that enable individuals to contract below the ground surface after flowering and to remain there at least until the following spring (Hughes 2005, Sivinski and McDonald 2007). Our field observations found that Winkler cactus individuals also contract to ground level or slightly below the surface following seed set. They emerge from below the ground surface and flower between April and mid-May, set seed by June, and begin to contract back beneath the ground surface for another year. In addition to the annual contraction, Winkler cacti often contract and remain underground for multiple years during drought conditions or when disturbed or damaged. When cacti go underground during the hot summer months, this reduces plant root temperatures to below lethal levels and increases survival (Garrett et al. 2010).

There have been a few studies on the life history of *Pediocactus* species; however, the work presented here is the only study conducted on Winkler cactus. Demographic studies on 2 other *Pediocactus* species have reported germination and growth rates (Spence 1993, Phillips and Phillips 2004, Hughes 2005, Shryock et al. 2014) and effects of large ungulate disturbance (Phillips and Phillips 2004). Shryock et al. (2014) present the only long-term study of a rare *Pediocactus* (*Pediocactus bradyi* L. Benson) with respect to population viability and climate change. Livestock impacts on other small cactus species have also been reported (Jiménez-Sierra et al. 2007, Hauser 2008, Coles et al. 2012). Induced climate change effects have been reported for another rare cactus, *Echinocactus platyacanthus*, in Mexico (Aragón-Gastélum et al. 2013).

We report here results from a 20-year study documenting basic demographic attributes and disturbance history of Winkler cactus. We use the data from this long-term study to address the following 2 questions: (1) What are typical growth rates, reproductive effort, and longevity of this species? (2) What is the relative role of disturbance by large ungulates and climate on flower production, recruitment, and plant mortality? Specifically, we analyze data on mortality, longevity, reproductive potential, recruitment, and presence of large ungulate trampling.

## METHODS

### Study Area

The study site is located in Capitol Reef National Park (Capitol Reef NP) in south central Utah. Winkler cactus occurs in the northern portion of the park and grows in soils associated with only a few geologic strata; it is generally found at elevations between 1493 m and 2134 m on low ridges and slopes in sparse desert shrub (DOI 2011).

Climate data from the weather station at Fruita, Utah (elevation 1692 m), approximately 16 air-kilometers south of the plot, were used in this study (NWS 2013). Climate within the Winkler cactus range is arid (150–200 mm mean annual precipitation) and warm (maximum average summer temperature 30 °C, minimum average winter temperature –3 °C). Average annual precipitation during the time-frame of this study was 203 mm. For the purposes of this study, we defined a water year as 12 months of precipitation, from April through March (Fig. 1a). This was done to correspond with Winkler cactus emergence and flowering.

In 1995 we established a 10 × 10-m monitoring plot in a location that contained enough cacti to support a long-term study of life history properties. The study site is located at 1823 m elevation on a low bench in the Brushy Basin member of the Morrison formation, and the soil best matches the Lybrook soil series. Plot aspect is southeast, slope is <5%, and the ground surface consists of fairly uniform fine gravel scattered with small- to moderate-sized black basalt boulders. Sparse vegetation cover consists of shadscale (*Atriplex confertifolia* (Torr. & Frém.) S. Watson), Mormon tea (*Ephedra torreyana* S. Watson), galleta grass (*Pleuraphis jamesii* Torr.), alkali sacaton (*Sporobolus airoides* [Torr.] Torr.), and prickly pear cactus (*Opuntia polyacantha* Haw.). Scattered large basalt rocks in the study area enabled us to step from boulder to boulder, thus reducing human disturbance.

The plot is in an active grazing allotment but has no established cattle trails or congregation points within or adjacent to it. Elk (*Cervus elaphus* Linnaeus) also use the area during winter months but usage is generally low.

### Data Collection

We collected data annually between April and mid-May when individual cacti were above

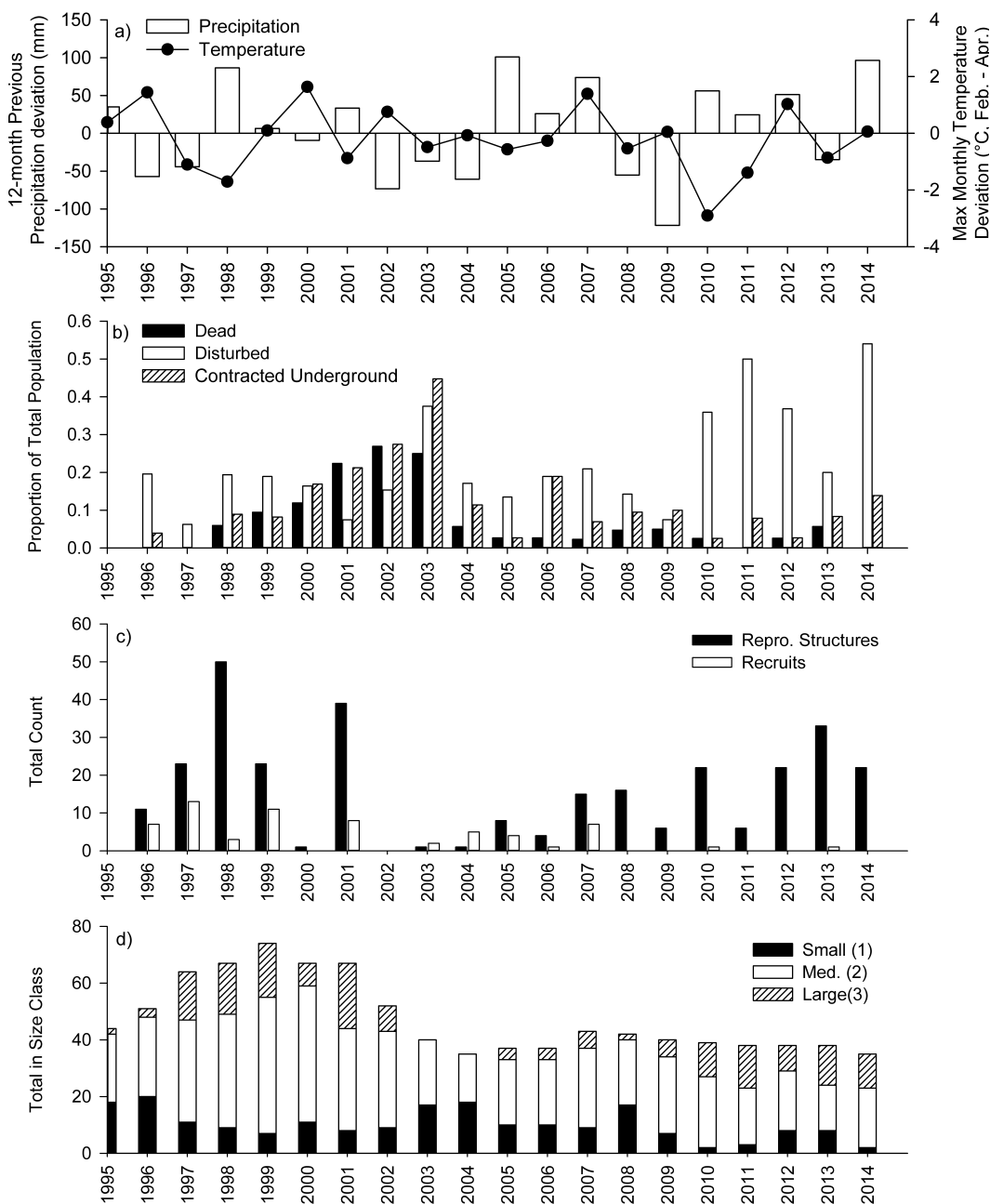


Fig. 1a. Deviation of precipitation from the average, plotted annually following the 12-month water year prior to April, overlain with the deviation of maximum monthly temperature from the average for February to April.

Fig. 1b. Proportion of Winkler cactus (*Pediocactus winkleri*) dead, disturbed, or underground, by year.

Fig. 1c. Number of reproductive structures and recruits (seedlings) for Winkler cactus (*Pediocactus winkleri*), by year.

Fig. 1d. Number of Winkler cactus (*Pediocactus winkleri*) by size class (small = SC1, medium = SC2, and large = SC3), by year.

ground and potentially reproductive. During data collection, the plot was gridded into 1-m squares, each cactus found was tagged and

mapped on graph paper, and every 1-m<sup>2</sup> plot was searched for new recruits. New cacti were marked with a tag and their locations mapped.

TABLE 1. Description of predictor variables in statistical models.

Predictor	Description	Type	df	Scale	Code
Current year disturbance	Whether plant was disturbed in observation year	binary	1	Individual	DIST
One-year disturbance	Disturbance 1 year prior	binary	1	Individual	PAST1
Two-year disturbance	Disturbance 2 years prior	binary	1	Individual	PAST2
Three-year disturbance	Disturbance 3 years prior	binary	1	Individual	PAST3
Past disturbance, no time	Whether a plant was disturbed at any time over the last 2 years, including current year (time invariant)	binary	1	Individual	PASTB
Past disturbance, count	Number of disturbances over the last 2 years, including current year (time invariant)	ratio	1	Individual	PASTC
Size class	Size of plant (3 size classes)	nominal	2	Individual	SIZE
April maximum temperature (°C)	Average maximum temperature in April	interval	1	Plot	MAXT
Feb–Mar minimum temperature (°C)	Average minimum temperature from February to March	interval	1	Plot	MINT
12-month prior precipitation (mm)	Sum of previous 12 months of precipitation, up to April	ratio	1	Plot	PPT12
April precipitation (mm)	Sum of precipitation in April	ratio	1	Plot	PPTAPR

Data collected annually on each marked cactus included the following: presence (present or absent); status (alive, dead, or underground); height and width; number of stems; number and stage (bud, flower, fruit) of reproductive structures; direct or indirect impacts (or both, within 2.5 cm); cactus damage (if any); and type and extent of damage. Damage categories included trampling by native or nonnative ungulates, rodent or beetle predation, or unknown cause. Cause of mortality was recorded if determinable. If a tag was found but there was no cactus, disturbances (if any) in the immediate area were recorded, and the individual was recorded as “absent” on the field datasheet. When recording disturbance to a cactus in the field, we differentiated 4 categories: mule deer (*Odocoileus hemionus* [Rafinesque]), elk, livestock, and unknown large ungulate (if track was indeterminate to elk or cattle). All cacti from each year were classified into 1 of 3 size-class categories by 1.0-cm increments for ease of organization and uniformity.

Because individuals can go underground for prolonged periods, tags were maintained at least 2 years after a recorded absence to mark each cactus’s location. This ability to

remain underground for multiple years made it difficult to determine the exact year of death and required us to create an “underground” category (Fig. 1b). Once an individual’s status was determined during subsequent field visits, (either by finding a carcass or a live cactus re-emerging), its status was updated to “alive” or “dead” (Fig. 1b).

#### Statistical Analysis

We formulated statistical models based on a simple set of hypotheses concerning cactus demographic responses to large ungulate disturbance and climate. The 3 responses we were interested in predicting were mortality, production of reproductive structures (flowers, buds, or fruits), and recruitment. Predictor variables were primarily divided into disturbance-related indicators, precipitation, temperature trends, and cactus size class (Table 1). In order to limit the number of candidate models and because there was no strong *a priori* evidence for more-complex models, we fitted simple 1, 2, and 3 main effects models, along with 2 main effects plus a single interaction model, where interaction terms were always between current year disturbance and a single climate variable.

TABLE 2. Fit statistics for models explaining cactus mortality from 1995 to 2014. Models are ranked by the difference ( $\Delta AIC_c$ ) between the top- and current-models. The negative log likelihood (LL), number of model parameters ( $K$ , includes random effects), and Akaike weights ( $w_i$ ) are also presented. DIST = current year disturbance, PAST1 = disturbance 1 year prior, PAST2 = disturbance 2 years prior, PASTB = binary occurrence of disturbance up to 2 years prior, MAXT = April maximum temperature, MINT = February–March minimum temperature, PPT12 = 12-month precipitation (cm), RE = random effects.

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	LL
DIST + MAXT + PASTB + DIST * MAXT + RE	7	454.1	0	0.27	-220.0
DIST + MAXT + PAST1 + PAST2 + DIST * MAXT + RE	8	455.4	1.33	0.14	-219.6
DIST + PAST1 + PAST2 + RE	6	456.3	2.23	0.09	-222.1
DIST + PAST1 + PAST2 + PPT12 + RE	7	456.6	2.49	0.08	-221.2
DIST + MINT + PAST1 + PAST2 + DIST * MINT + RE	8	456.9	2.86	0.06	-220.4
DIST + PASTB + MAXT + RE	7	457	2.88	0.06	-221.4
DIST + PAST1 + PAST2 + MAXT + RE	7	457	2.88	0.06	-221.4
PASTB + RE	4	457.6	3.49	0.05	-224.8
DIST + PPT12 + PAST1 + PAST2 + DIST * PPT12 + RE	8	457.8	3.75	0.04	-220.8
DIST + PAST1 + PAST2 + MINT + RE	7	458.1	3.98	0.04	-222.0
PASTB + MAXT + RE	5	458.1	3.98	0.04	-224.0
RE (null model)	3	466.41	12.32	0	-228.0

Predictor variables were informally inspected for correlation with scatterplots in order to reduce any confounding effects from collinearity prior to model fitting. For the purposes of this analysis only elk, livestock, and unknown large ungulate disturbances were considered, and these categories were combined into one “disturbed” category.

#### Model Fitting and Comparison

We used a generalized linear repeated measures mixed effects (GLMM) procedure to fit individual cactus responses, treating sampling year as a random effect and other covariates as fixed effects. We modeled mortality and flowering as binary variables using the logistic link function to model covariate effects on the probabilities of dying and flowering. Models were fitted in R using the lme4 package (version 0.999375-42; Bates et al. 2013). We fit a total of 28 candidate models for mortality and 26 candidate models for flowering.

It was not possible to associate recruitment of new cacti to individual cactus flowering events; thus, the probability of recruitment was assessed at the plot level. We examined the relationship between total recruitment and the number of reproductive structures 1–5 years prior to observation, in addition to the climate and disturbance variables described in Table 2, with Pearson correlations. (R Development Core Team 2013).

We adopted an information-theoretic approach to comparing and selecting multiple competing models (Burnham and Anderson

2002). Models for mortality and flowering were ranked and compared using Akaike’s information criterion adjusted for small sample sizes ( $AIC_c$ ) to narrow the candidate model set. Models within a cumulative Akaike weight ( $w_i$ ) of  $<0.95$  were considered to have strong support for further analysis, resulting in a number of nested models being considered competitive with the top model for all response variables. Such a situation suggests that potentially uninformative predictor variables are within  $0.95w_i$  (Arnold 2010); thus, parameters from models within the  $0.95w_i$  of the top-weighted model were averaged together and their coefficients, standard errors, and odds ratios were estimated with the MuMIn package in R (version 1.9.13; Barton 2013). If the set of top-weighted models contained interactions, their coefficients were estimated both with and without the interaction present. We considered effect sizes to be statistically compelling enough to draw inferences if the 85% confidence intervals for odds ratios did not overlap 1. Predicted probabilities of flowering and mortality were then estimated as a function of the composite model that included predictor variables in the competitive model set.

#### Model Evaluation

While  $AIC_c$  values can be used to narrow a large set of candidate models to a handful of competing hypotheses,  $AIC_c$  cannot ultimately distinguish between good-fitting and poorly fitting models. We used goodness of fit, assessed numerically using area-under-the-curve (AUC)

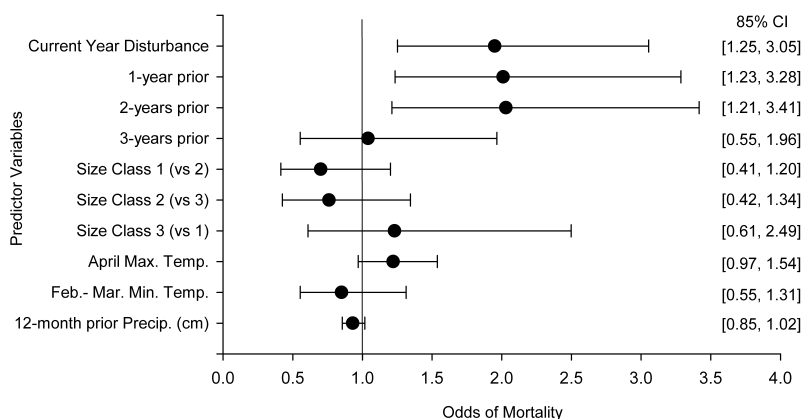


Fig. 2. Mean odds (black circles) of mortality with 85% confidence intervals (error bars), by predictor variables from the top-ranked model set. Values  $>1$  suggest mortality increases with increases in the predictor, whereas values  $<1$  suggest mortality decreases with increases in the predictor. Odds ratios that are indistinguishable from 1 (i.e., their confidence intervals include 1) do not likely affect mortality.

and Somer's  $D$  ( $D_{xy}$ ), to examine the performance of top-weighted models. The AUC is the most commonly reported model fit value for binary classifications and can be interpreted as the proportion of events that are correctly predicted by a model. Any AUC values near 0.5 are considered to be poor fits (no better than chance), whereas a value of 1 implies perfect fit. Somer's  $D$  is related to AUC but describes the overall power of the model to distinguish between events (i.e., cactus death or cactus flowering) and nonevents (i.e., no death or no flowering). The  $D_{xy}$  values range from 0 to 1, with 1 being perfect discrimination (i.e., every single event is correctly attributed by the model to what was observed in the data set) and 0 suggesting random discrimination. The AUC and Somer's  $D$  were evaluated from models that (1) only included predictors within the  $0.95w_i$  set; and (2) only included predictors if their 85% odds ratio confidence intervals did not overlap 1.0 (MuMIn version 1.9.13, Barton 2013).

## RESULTS

### Population Structure and Dynamics

In 1995 we tagged 44 live cacti. The cactus population peaked in 1999 with 67 known live cacti but has since been declining. By 2014, only 31 live cacti remained in the plot and 5 cacti known to be alive in 2013 were absent/underground (Fig. 1b). Over the course of this study a total of 71 plants died, which

represents an overall 18% decline in the plot population. Since 2008, recruitment has occurred in only 2 years (2010 and 2013; Fig. 1c), whereas mortality events have occurred 5 out of the 7 years (range 3%–6%; Fig. 1b).

The majority of cacti measured (59% on average) fell into the medium size class (between 1.1 cm and 2.0 cm in diameter, size class 2; Fig. 1d). A few (14%) of the tagged cacti recorded an increase in size of  $>2$  cm over the course of this study, whereas most cacti (86%) exhibited either no growth or only a size increase of  $<1$  cm. Approximately 5% of tagged cacti grew an additional stem during their lifespan and another 5% grew a secondary stem on top of the existing stem. The new secondary stems may be seedlings that germinated on top of the parent plant. Neither of these occurrences were correlated with plant damage or disturbance but rather appeared to be due to longevity.

Winkler cactus longevity is still being determined, as we found substantial variation depending on environmental conditions and impacts to individual cactus. Over the course of this study, 34 (32%) cacti lived 10 years or longer. Five of the originally tagged cacti are still alive. Of these 5, two were  $>1.4$  cm in diameter when tagged in 1995, indicating they were adult plants at that time.

### Disturbance and Mortality

The proportion of live cacti disturbed by large ungulates (elk and livestock) varied year

to year, from a low of 5% in 1997 to more than 50% in 2014 (Fig. 1b). The highest mortality rates were recorded between 1999 and 2003 (Fig. 1b). Over the course of this study, 27 cacti died of unknown causes (although 2 of these are suspected of dying from rodent predation). Two cacti were damaged by an unidentified insect; one died and the other survived. The remaining 43 cacti that died were disturbed by ungulates sometime during their lifespan; 25 by livestock, 5 by deer, 9 by elk, and 4 by unidentified large ungulates. Of the 107 individual cacti tagged since 1995, 74 were disturbed at least once by large ungulates, excluding deer. Some of these were disturbed more than once, resulting in 205 recorded incidences of disturbances. There were 10 incidences of elk disturbance and 5 incidences by unidentified large ungulates. The remaining 190 (93%) disturbance incidences were attributable to livestock.

Model results strongly suggest there was a cumulative effect on mortality from multiple disturbances. Disturbances during the current year, 1 year prior, and 2 years prior were present in several of the final 11 competitive models (Table 2). If a cactus was disturbed in the current year, the odds of it dying were 1.95 times higher than for an undisturbed cactus (Fig. 2). Similarly, the odds increased slightly for cacti disturbed 1 year (odds ratio = 2.01) or 2 years prior (odds ratio = 2.03; Fig. 2). The probability of a cactus dying if not disturbed was 3%, but the cumulative effect if disturbed twice was a 9% probability of dying and, if disturbed 3 times during any 3-year period, a 17% probability of dying (Fig. 3a).

Statistical model results provide evidence that weather variations also contributed to cactus mortality. While models containing only weather effects were not solely included within the competitive model set, confidence intervals from model averaging highlighted precipitation and temperature effects on mortality (Table 2, Fig. 2). High mortality rates occurred between 1999 and 2003 (Fig. 1b), roughly following drought years in south central Utah from 1998 through 2004. During this time period, we also recorded the largest number of cacti remaining underground (Fig. 1b). Analysis showed that there was a slight increase in the probability of cacti dying as the April maximum temperatures increased (regardless of disturbance) (Fig. 3b). Cacti

disturbed 3 times over 3-year intervals were even more likely to die as April maximum temperatures increased (Fig. 3c).

Conversely, there was a small decrease in odds of dying with increasing precipitation (12-month previous precipitation odds ratio = 0.93) regardless of disturbance (Fig. 2). Model fit from model-averaged parameter estimates was good, with an AUC of 0.85 for an overall model that included all parameters within the competitive model set (cumulative  $w_i < 0.95$ ): disturbance + 1-year past disturbance + 2-year past disturbance + maximum temperature + precipitation 12 months prior (Table 2). The discriminating power of the model was fair ( $D_{xy} = 0.68$ ), with the model accurately predicting living cactus numbers but overestimating the number of dead cacti within the data set.

### Flowering

During this study, an average of 28% of cacti produced reproductive structures (buds, flowers, or fruits) in a given year, and each cactus produced an average of 1.43 structures. Only 7 of the 107 cacti tagged produced 3 or more reproductive structures in a given year, and just 10% of cacti that flowered produced 2 or more flowers in a season. Of the 34 cacti that were recorded alive for 10 years or longer, 3 (9%) never flowered and 6 (18%) flowered only once.

The final model sets for predicting flowering included 3 competitive models (Table 3). Model results suggest that current year disturbance by large ungulates decreased the odds of a cactus flowering by 53% (odds ratio = 0.47) compared to an undisturbed cactus (Fig. 4a). The probability of a cactus flowering following disturbance was reduced regardless of size class (Fig. 5a). When the disturbance occurred in prior years, odds of flowering appeared to decrease relative to current year disturbance; however, these confidence intervals all overlap 1.0 (Fig. 4a).

Cacti  $\geq 2.1$  cm in diameter (size class 3) flowered far more frequently than cacti  $< 2.0$  cm (size class 1 and 2) in diameter (Fig. 4b). When all 3 size classes were combined, the probability of cacti flowering increased during wet years (Fig. 5c) and decreased slightly as April maximum temperatures increased (Fig. 5b). The odds of flowering increased by 8% for every 10 mm of precipitation (odds ratio

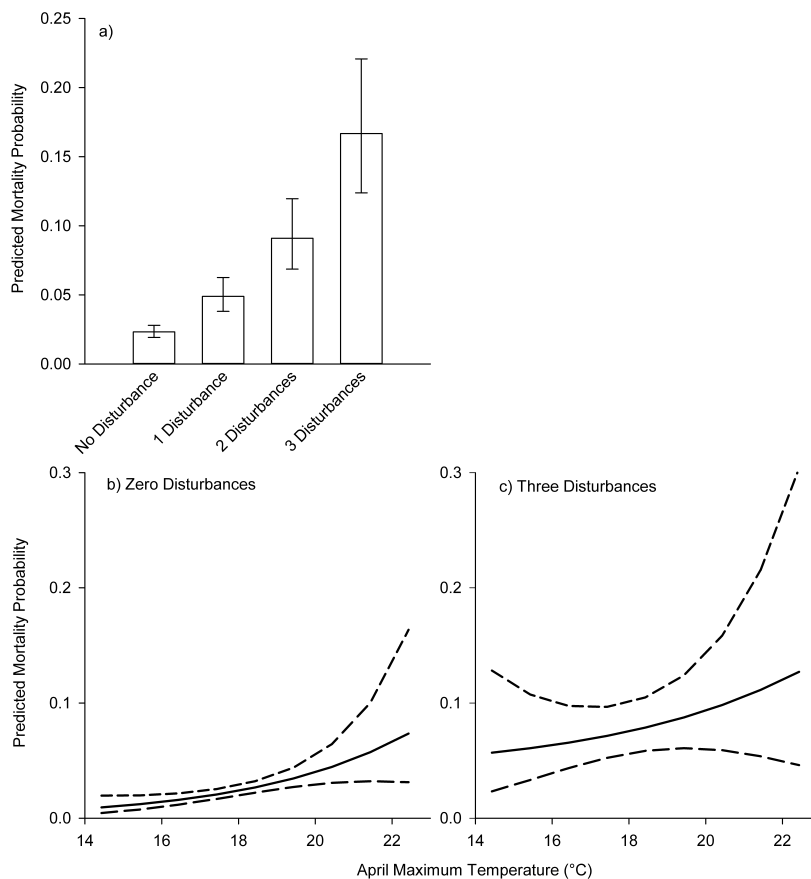


Fig. 3a. Estimated mortality probabilities for 0, 1, 2, and 3 disturbances in any 3-year period. Error bars for 85% confidence intervals are shown. Mortality probabilities are estimated from the composite model (mortality probability = disturbance + 1 year past disturbance + 2 years past disturbance + maximum April temperature + 12-month precipitation); continuous predictor variables (i.e., temperature, precipitation) are held at their observed mean values for the study period.

Fig. 3b. Predicted mortality probability by April maximum temperature for cacti with no disturbance. Graphical output for mortality models is based on overall model-averaged regression parameters from top-ranked models (i.e., cumulative  $w_i < 0.95$ ; mortality probability = disturbance + 1 year past disturbance + 2 years past disturbance + maximum April temperature + 12-month precipitation). Mean response (solid line) and 85% confidence intervals (dashed lines) are shown. The mean predicted response is shown as a function of April maximum temperatures observed during the study for undisturbed cacti during any 3-year period. Other continuous predictor variables are held at their observed means during the time period (i.e., precipitation).

Fig. 3c. Predicted probability by April maximum temperature for cacti disturbed 3 times. Graphical output for mortality models is based on overall model-averaged regression parameters from top-ranked models (cumulative  $w_i < 0.95$ ). Mean response (solid line) and 85% confidence intervals (dashed lines) are shown. The mean predicted response is shown as a function of April maximum temperatures observed during the study for cacti disturbed 3 times over any 3-year period. Other continuous predictor variables are held at their observed means during the time period (i.e., precipitation).

= 1.08) (Fig. 4a). The odds of cacti flowering also increased following warmer February–March minimum temperatures (Figs. 4a, 5d). Model fit from model-averaged parameter estimates was high, with an AUC of 0.88 for an overall model that included all parameters within the top-ranked models (cumulative  $w_i < 0.95$ ):

disturbance + minimum temperature + maximum temperature + precipitation 12 months prior + size class (Table 3). The discriminating power of the model was also high ( $D_{xy} = 0.75$ ), with the model accurately predicting reproductive cactus events across a majority of the data set.



TABLE 3. Fit statistics for models explaining cactus reproduction from 1995 to 2014. Models are ranked by the difference ( $\Delta AIC_c$ ) between the top and current models. The negative log likelihood (LL), number of model parameters ( $K$ , includes random effects), and Akaike weights ( $w_i$ ) are also presented. DIST = current year disturbance, SIZE = size class, MAXT = April maximum temperature, MINT = February–March temperature, PPT12 = 12-month precipitation (cm), RE = random effects.

Model	$K$	$AIC_c$	$\Delta AIC_c$	$w_i$	LL
DIST + SIZE + RE	6	803.7	0	0.70	-395.8
PPT12 + MAXT + SIZE + RE	7	806.3	2.59	0.19	-396.1
PPT12 + MINT + SIZE + RE	7	808.8	5.07	0.06	-397.3
RE (null model)	3	924.6	120.86	0	-459.3

### Recruitment

Recruitment of new Winkler cactus occurred only sporadically during this 20-year study (Fig. 1c). There was a moderate correlation between the number of reproductive structures produced to the number of recruits found the following year (Pearson's  $r = 0.57$ ,  $n = 18$ ,  $P = 0.07$ ). The relation between these 2 factors suggests that high recruitment events have some correlation with high flowering events; however, analysis of this relationship was greatly affected by zero recruitment and high flowering events.

Recruitment was correlated with warmer minimum temperatures in February and March (Pearson's  $r = 0.53$ ,  $n = 18$ ,  $P = 0.015$ ). Between 2006 and 2013, the minimum February and March temperatures in the study area were below  $-1^\circ\text{C}$  for  $\geq 30$  days in this 2-month period. During this 9-year span, 10 new recruits were recorded. During the previous 10-year time span, only half the years had  $\geq 30$  days below  $-1^\circ\text{C}$ , and 53 new recruits were recorded.

Correlations between recruitment and disturbances during the current year (Pearson's  $r = -0.36$ ,  $n = 18$ ,  $P = 0.124$ ), 1 year previous ( $r = -0.07$ ,  $n = 18$ ,  $P = 0.77$ ), and 2 years previous ( $r = -0.32$ ,  $n = 18$ ,  $P = 0.168$ ) were all negative but ultimately not significant.

### DISCUSSION

The long-term data set on Winkler cactus presented here provides new insights into cactus demographic trends and the relative role of large ungulate disturbances and weather variations. This type of information is critical for management agencies tasked with ensuring long-term survival of this rare species.

During surveys throughout the range of Winkler cactus, we occasionally observed an individual cactus much larger (5 cm in diame-

ter with as many as 5 flowers occurring on a single-stemmed plant) than the largest cacti in our study plot. Because individual cacti in the plot known to be at least 20 years old were no larger than 3.7 cm diameter, the larger cacti observed outside the study area suggest that some members of this species may either be very long lived (much longer than 20 years) or have growth rates that are faster than observed in this study. Growth rate variations related to climate have been reported on other cactus species by Drezner (2005) and Aragón-Gastélum et al. (2013). Phillips and Phillips (2004) summarized a 20-year data set on Peebles Navajo cactus (*Pediocactus peeblesianus* var. *peeblesianus* [Croizat] L.D. Benson) and reported that flowering was observed in individuals 1.4 cm in diameter or larger. Cacti of this size in their study were considered adult plants between 10 and 15 years old. Warren et al. (1992) reported that Houserock cactus (*Pediocactus paradinei* B.W. Benson) reaches reproductive maturity around 10 years of age with a potential maximum lifespan of more than 40 years. These results are similar to our findings that Winkler cacti 2 cm in diameter or larger are probably 15 years or older, and individuals reaching 5 cm in diameter may be closer to 40 years old.

We found that most (68%) Winkler cacti did not live beyond 10 years and, of those that did live longer than 10 years, 27% produced few flowers during their lifetime. Additionally, a very few long-lived (and therefore larger) cacti produced a large proportion of the flowers we observed during the 20-year study. This pattern of larger cacti producing more flowers per stem than do smaller individuals has been observed in another species (Brady pincushion cactus, *P. bradyi*; Spence 1993, Hughes 2005, Shryock et al. 2014) and has significant implications for Winkler cactus population sustainability. In this study, the few

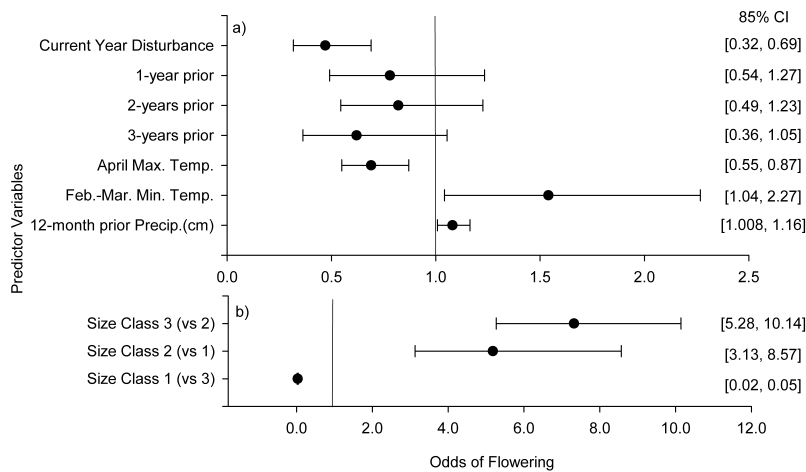


Fig. 4a. Mean odds of flowering (black circles) with 85% confidence intervals (error bars), by predictor variables from the top-ranked model set. Values  $>1$  suggest that flowering increases with increases in the predictor, whereas values  $<1$  suggest that flowering decreases with increases in the predictor. Odds ratios that are indistinguishable from 1 (i.e., their confidence intervals include 1) do not likely affect the odds of flowering.

Fig. 4b. Odds of flowering by size class from the competitive model set. Values  $>1$  suggest a positive relationship between the response and predictor variable, whereas values  $<1$  suggest a negative relationship. Confidence intervals that include 1 are considered to have no or marginal effects on flowering.

large ( $\geq 2.1$  cm diameter) Winkler cacti with high reproductive potential appear crucial to sustaining the population over the long term. Thus, factors that increase these individuals' probability of mortality may put the sustainability of small, isolated populations at risk.

One of the most striking findings of this study is the overall low fecundity of Winkler cactus in our plot. Our study found that cacti 0.5 cm in diameter rarely flower and only 5% of tagged cacti between 0.5 cm and 1.0 cm were reproductive during the entire 20-year study. Twenty percent of individual cacti did not flower during this entire study; one of these was a cactus that lived 18 years. The reproductive output that does occur is concentrated in only a few individuals. For example, only 5 cacti (15%) alive at least 10 years flowered more than 50% of the time. In addition, 10 cacti produced 31% of all flowers (during the entire study) and nearly half (49%) of these flowers were produced by only 3 cacti.

The 3 most prolific flowering cacti grow underneath shrubs or between rocks that have protected these individuals from disturbance. In addition, these cacti may receive protective benefits from the shrubs or rocks in the form of soil moisture conservation, moderation of soil temperatures, reduction of solar radiation,

or any combination. Many cactus species are closely correlated with nurse plants, including small globose cacti similar to *Pediocactus* (Withgott 2000, Mandujano et al. 2002, Godinez-Alvarez et al. 2003); however, there are no literature references to *Pediocactus* and nurse plants or nurse rocks. Peters et al. (2008) found increased longevity and growth rates of *Mammillaria* spp. when individual cactus grew directly adjacent to nurse rocks rather than underneath nurse shrubs. Further study of the association between Winkler cactus and nurse plants or rocks is warranted.

In conjunction with the low flowering rate, recruitment rates were sporadic and low. Our findings were similar to those of Sivinski and McDonald (2007) and Phillips and Phillips (2004), who found that recruitment of *Pediocactus* in their long-term studies was not consistent from year to year but rather was episodic. Spence (1993) reported that Brady pincushion cacti were probably 2–3 years old before emerging above ground, which makes linking recruitment events to flowering rates difficult. Low reproductive potential has been implicated as a causal factor limiting colonization of unoccupied habitat in a similar species (Houserock cactus; Warren et al. 1992). Additionally, seeding trials suggest that

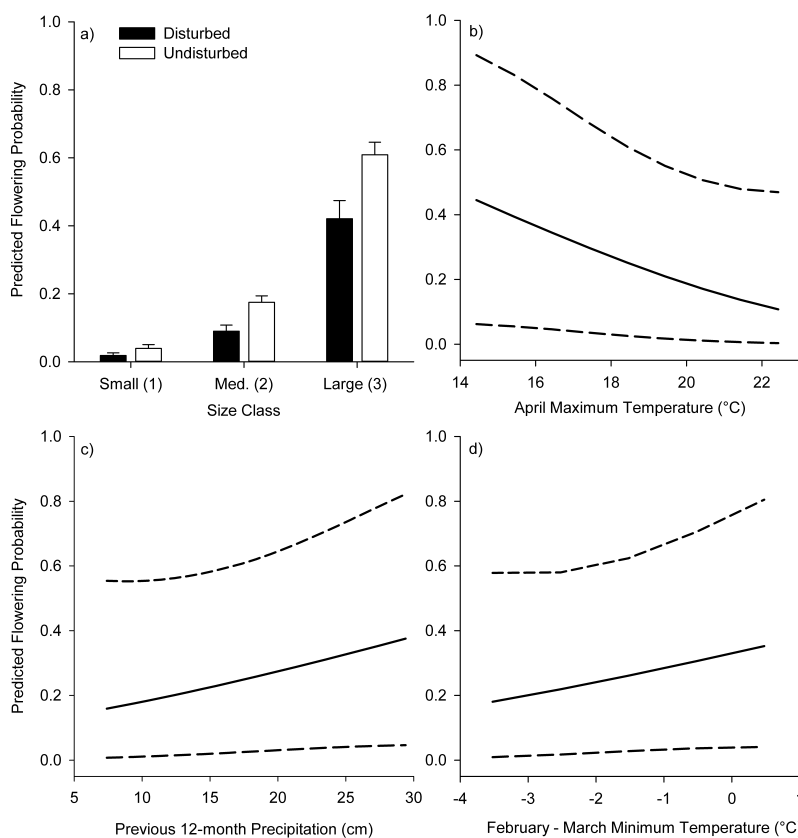


Fig. 5a. Estimated flowering probabilities for disturbed and undisturbed cacti, by size class. Error bars for 85% confidence intervals are shown. Flowering probabilities are estimated from the composite model (flowering probability = disturbance + minimum February–March temperature + maximum April temperature + 12-month precipitation + size class); continuous predictor variables (i.e., temperature, precipitation) are held at their observed mean values for the study period.

Fig. 5b. Estimated flowering probabilities for both disturbed and undisturbed cacti, across all size classes, as a function of April maximum temperatures. Mean response (solid line) and 85% confidence intervals (dashed lines) are shown. Flowering probabilities are estimated from the composite model (flowering probability = disturbance + minimum February–March temperature + maximum April temperature + 12-month precipitation + size class); continuous predictor variables (i.e., temperature, precipitation) are held at their observed mean values for the study period.

Fig. 5c. Estimated flowering probabilities for both disturbed and undisturbed cacti, across all size classes, as a function of precipitation over the previous 12 months. Mean response (solid line) and 85% confidence intervals (dashed lines) are shown. Flowering probabilities are estimated from the composite model (flowering probability = disturbance + minimum February–March temperature + maximum April temperature + 12-month precipitation + size class); continuous predictor variables (i.e., temperature, precipitation) are held at their observed mean values for the study period.

Fig. 5d. Estimated flowering probabilities for both disturbed and undisturbed cacti, across all size classes, as a function of February to March minimum temperatures. Mean response (solid line) and 85% confidence intervals (dashed lines) are shown. Flowering probabilities are estimated from the composite model (flowering probability = disturbance + minimum February–March temperature + maximum April temperature + 12-month precipitation + size class); continuous predictor variables (i.e., temperature, precipitation) are held at their observed mean values for the study period.

a related species (Knowlton's cactus, *Pediocactus knowltonii* L.D. Benson) has very low germination rates, with few new seedlings (4%) becoming established (Sivinski and McDonald 2007). Our findings are consistent with these previous studies and suggest that multiple factors affect successful recruitment.

A low germination and establishment rate coupled with a 2- to 3-year delay for appearance of seedlings above ground could explain why the recruitment analysis (Table 3) does not show a strong correlation between flowering and the first appearance of seedlings. More research is needed to determine precisely

what factors most affect recruitment, especially with regard to drivers of successful seed germination.

Our study specifically looked at large ungulate disturbances to Winkler cactus to determine whether these disturbances affected flowering or survival of individual cacti. The results presented here, which suggest that disturbance of Winkler cactus by large ungulates increases probability of mortality and decreases probability of flowering, are similar to results of disturbance analysis for other cactus species. Coles et al. (2012) also reported that livestock and horse grazing at any time of year in areas occupied by Mesa Verde fishhook cactus (*Sclerocactus mesae-verdae* [Boissev. & C. Davidson] L.D. Benson) is detrimental to that small, globose cactus. They attributed this detriment to direct trampling, displacement of large amounts of soil, disruption of soil structure, and burying of seed banks when large ungulates walk across wet clay soils (Coles et al. 2012). Our field observations found that the most prolific flowering cacti in the plot were growing in protected locations (under shrubs or between large rocks). These results suggest that large ungulate (primarily cattle in our study) disturbances can reduce the long-term survival of Winkler cacti by increasing the mortality rates and decreasing the reproductive rates.

The Four Corners region of the United States has been in varying degrees of drought for over a decade, and current climate change predictors suggest this new precipitation regime may become the new normal (U.S. Global Change Research Program 2014). Limited research has been conducted on climate and weather variations with regard to cactus species (Parker 1993, Godínez-Álvarez et al. 2003, Téllez-Valdés and Dávila-Aranda 2003, Drezner 2005, Aragón-Gastélum et al. 2013, Spector 2013, Shryock et al. 2014). Hughes' (2005) study on Brady pincushion cactus correlated reduced seed set with below-average precipitation during the time prior to cactus seeding. Sivinski and McDonald (2007) reported that Knowlton's cactus consistently contracted underground during severe drought periods. Shryock et al. (2014) reported that high-precipitation events correlated with higher germination rates for Brady pincushion cactus but that long-term survival of seedlings was closely related to a more moderate temperature

regime (lower summer temperatures and higher winter temperatures). These findings closely match our study results for Winkler cactus.

Weather variations observed during this study appear to be affecting Winkler cactus, and these results have implications for the future of the species in the face of potential climate change. For example, we found that higher maximum April temperatures increase the probability of cactus mortality (Fig. 3b, 3c). The increased mortality associated with higher April temperatures may be because plants are typically above ground and flowering in April, making them susceptible to increased stress (Spector 2013). During the hottest months of the year, the cacti are typically below ground and insulated from the heat (Garrett et al. 2010).

Conversely, warmer minimum temperatures during February and March resulted in an increase in recruitment. Warmer temperatures during these months may give the newly sprouted cactus an increased chance of survival. Our analysis of many of the factors affecting recruitment was inconclusive and suggests that there are many other parameters that affect successful germination and survival of Winkler cactus seedlings.

The positive relationship between survival of Winkler cacti and higher precipitation found in this study (Fig. 2) is corroborated by studies on other cactus species. Shryock et al. (2014) reported higher survival rates for Brady pincushion cactus during years of higher precipitation. Other researchers have found a positive relationship between moisture availability and growth rate of Saguaro cactus (*Carnegiea gigantea* [Engelm.] Britton & Rose) (Parker 1993, Godínez-Álvarez et al. 2003, Drezner 2005), but these studies did not examine survival. Though not tested statistically, we observed that periods with low rainfall were correlated with higher numbers of cacti remaining underground (e.g., 2000 through 2003; Fig. 1b). The degree to which remaining underground for one or more growing seasons affects cactus physiology has not been documented in the literature but undoubtedly would reduce an individual's energy stores and subject it to increased mortality. The relationships observed here between weather variability and cactus demographic parameters suggest that, if the climate pattern observed during recent years

of reduced precipitation, hotter April maximum temperatures, and colder February–March minimum temperatures continues, Winkler cactus populations are likely to experience increased mortality coupled with a pronounced reduction in flowering and recruitment.

Although 20 years provides a very long data set of detailed measurements, additional study is needed to more completely understand environmentally driven changes in population structure and dynamics for Winkler cactus. In addition, other unmeasured processes may be important in understanding the relationships between causal factors and population demographics.

Our study was limited to a single site; however, the effects of weather variations and large ungulate disturbances are likely similar for many Winkler cactus localities. Therefore, factors that increase mortality, such as disturbance from large ungulates, combined with stressors of weather variation, low fecundity rate, and small, isolated occurrences, suggest that long-term persistence of some Winkler cactus populations is uncertain. Based on our findings, we conclude that Winkler cactus populations protected from large ungulate disturbance, particularly during drought years, are more likely to persist over the long-term. In addition, we determined that several weather variables affect Winkler cactus demographic parameters. More work is needed to understand how these weather variables will change under future climates and what effects such changes will have on the survival of the species.

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Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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