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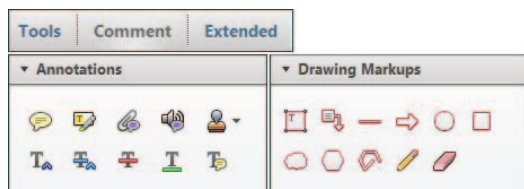
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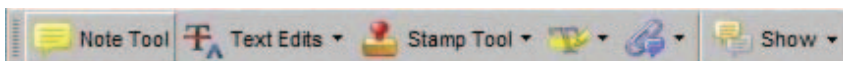
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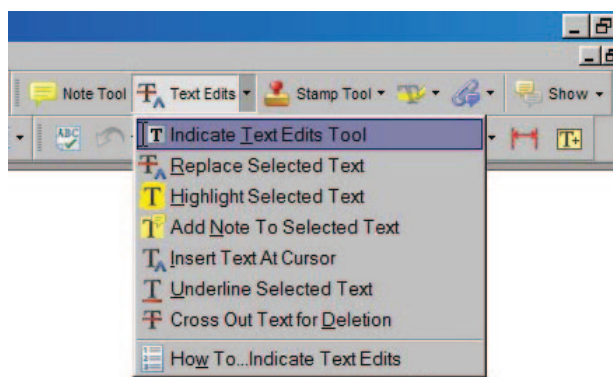
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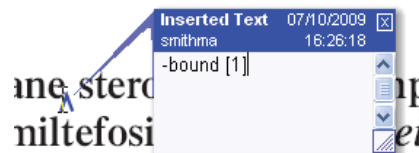
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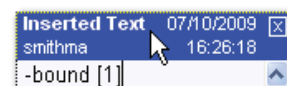
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Characterizing predictors of survival in the American pika (*Ochotona princeps*)

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The measurement of stress hormone (glucocorticoid [GC]) concentration is increasingly used to assess the health of wildlife populations. However, for many species, we do not have a good understanding of the range of GC concentrations that might indicate a compromised individual. A temporary increase in GC concentration can prompt the adoption of behavior or activities to promote individual survival. However, chronic GC elevation results in deleterious effects on health that can reduce survival. In order to use GC concentration as a metric of individual fitness for a given species, it will be necessary to relate individual demographic rates to GC concentration. We related survival in American pikas (*Ochotona princeps*) to 2 different stress metrics, glucocorticoid metabolite (GCM) concentration in fecal samples and GC concentration in plasma samples. Annual survival was analyzed in relation to each of these stress metrics as well as other physiological metrics and habitat characteristics at several sites in the Rocky Mountains. Among the predictors considered, GCM concentration was by far the strongest predictor of annual survival in pikas, and individuals with higher baseline GCM were less likely to survive. Our metric of flea load was also negatively related to annual survival. Given the limited time and resources that characterize many wildlife conservation projects, it is important to establish which endocrine metrics are the most informative for a species. American pikas have been identified as a sentinel species for detecting effects of climate change, and several correlational studies have projected range contraction for the species. Our results suggest that more mechanistic projections might be possible given further study of the relationship between GCM and climate. Our approach contributes to a better understanding of factors affecting survival in this species and provides a basis for further research relating individual stress response and survival to environmental change.

Key words: climate change, ecophysiology, glucocorticoids, mark-resight, Rocky Mountains, sentinel species, stress response

The endocrine condition of an animal correlates with its health, and the measurement of stress hormone (glucocorticoid [GC]) concentration is often used to assess the health of a population (Wingfield et al. 1994; Creel et al. 1996; Wasser et al. 2000; Romero 2004). However, for most populations, we do not know how high or how long GC concentration must rise to do harm. An increase in GC secretion typically enables an animal to redirect behavior, an adaptive response which may result in a favorable outcome for many individuals (Sapolsky et al. 2000). Thus, elevated GC concentration does not always indicate distress (Moberg 2000; Romero 2004), and an evolved stress response is often what allows an individual to cope with environmental change or stochastic events. Some studies have

suggested that elevation of GC concentration provides adaptive advantages to the individual such as enhanced survival or reproductive opportunities (Boonstra et al. 2001; Cote et al. 2006). Others show that chronic elevation of GC concentration results in deleterious effects that ultimately reduce survival, such as diminished resistance to disease, or impaired growth and development (Sapolsky et al. 2000; Romero and Wikelski 2001; Rogovin et al. 2003). Additionally, it is generally accepted that an increase in GC concentration leads to a reduction in reproductive activities in favor of self-preservation behaviors, therefore promoting individual survival over current reproductive success (DeNardo and Licht 1993; Breuner and Hahn 2003; Lanctot et al. 2003; Lynn 2003; Breuner et al. 2008).

To better interpret the consequences and ultimate effects of varying GC concentration, it is necessary to understand how individual demographic rates relate to GC concentration.

2.5 Due to the numerous adverse consequences previously men-
 2.10 tioned, high baseline GC concentration should be negatively
 2.15 associated with metrics of relative fitness such as survival. For
 2.20 example, a recent review (Bonier et al. 2009) found that base-
 2.25 line GC concentration was negatively correlated with survival
 in approximately half of the studies involving diverse bird
 and animal species, such as marine iguanas, cliff swallows,
 and ring-tailed lemurs. However, approximately 1 quarter of
 the studies reported a positive correlation between baseline
 GC concentration and survival, as exhibited in side-blotched
 lizards, European starlings, and European wild rabbits. In
 the remaining quarter of the studies, there appeared to be no
 relationship between survival and baseline GC concentration
 for several other species including European white storks and
 yellow-legged gulls (Bonier et al. 2009). These findings sug-
 gest that survival can be predicted by baseline GC concentra-
 tion, but the relationship is not consistent across all species.
 Many factors related to life-history strategies can confound
 interpretation of GC concentration, such as predator pressure
 (Clinchy et al. 2004), reproductive status (Boonstra et al. 1998),
 and social structure of the population (Gobush et al. 2008).
 Increased GC concentration may be an indicator of a popula-
 tion in distress, but we must first understand the relationship
 between the magnitude of GC secretion and metrics of indi-
 vidual performance for a species.

2.30 Here, we related survival in American pikas (*Ochotona*
princeps) to 2 different stress metrics, plasma GC concentra-
 tion in blood samples and glucocorticoid metabolite (GCM)
 concentration in fecal samples. The American pika (hereafter,
 pika) is a cold-adapted lagomorph occurring only in rocky areas
 of the western United States and Canada. Pikas rely on access
 2.35 to cool subsurface microclimates to escape warmer tempera-
 2.40 tures and are widely considered a sentinel species for detect-
 ing ecological effects of climate change (McDonald and Brown
 1992; Hafner 1993, 1994; Lawlor 1998; Beever et al. 2003;
 Smith et al. 2004; Grayson 2005). In the Great Basin, the low-
 est elevation of pika occurrence has risen 150 m during the last
 century and climate change has been implicated as a contribut-
 ing factor of recent population losses in this area (Beever et al.
 2.45 2010, 2011; Wilkening et al. 2011). Throughout the western
 United States, pikas may lose 55% (95% CI = 35–66%) of their
 potential range even under low emission scenarios (Ray et al.
 2012), and the species has been considered for listing as threat-
 ened or endangered at both federal and state levels (United
 States Fish and Wildlife Service [USFWS] 2010; Osborn and
 Applebee 2011).

2.50 Survival can be influenced by a species' response to both
 acute and chronic stress, so considering metrics of both should
 improve overall understanding of the stress response (Breuner
 et al. 2008; Bonier et al. 2009). By measuring GC concen-
 2.55 tration in plasma samples and GCM concentration in fecal
 2.56 samples, our study design allowed for the inclusion of both
 acute and chronic (baseline) stress metrics. GCs travel to their

target tissues via the blood, and plasma GC concentration can
 increase rapidly in response to a stressor (Cook et al. 2000;
 Romero 2004). Blood samples were collected from individuals
 more than 3 min after initial capture during a period of acute
 stress resulting from the capture, confinement, and handling
 process; thus, our plasma GC concentration represents an acute
 stress metric. Fecal samples collected during the same handling
 process, however, reflect average GC concentration during the
 pika's normal activities, 10–12 h prior to capture (Wilkening
 et al. 2013). Fecal samples, therefore, were used to infer base-
 line GCM concentration or chronic stress response. We also
 analyzed individual survival in relation to other indicators of
 physiological condition (weight, ectoparasite load) and habitat
 characteristics (elevation, slope aspect) suggested to affect pika
 population dynamics (Biggins and Kosoy 2001; Rodhouse et al.
 2.70 2010; Jeffress et al. 2013; Yandow et al. 2015). We hypothesized
 that the probability of survival would be higher for individuals
 with lower GCM, under the assumption that these pikas were
 experiencing lower levels of chronic physiological stress. We
 2.75 also hypothesized that survival would be higher for pikas with
 higher GC, under the assumption that an acute stress response
 facilitates appropriate reaction to a stressor. A failure to release
 GCs into the bloodstream in response to a stressful event could
 indicate poor health or other factors leading to low survival
 2.80 (Busch and Hayward 2009). Finally, we hypothesized that sur-
 vival would be higher for individuals with higher weights and
 fewer ectoparasites, and those living in microhabitats charac-
 terized as more suitable in previous studies.

2.85

MATERIALS AND METHODS

Study area and sample collection.—Pikas were sampled at
 5 sites in the Rocky Mountains: Emerald Lake (EL) and Swan
 Creek (SC) in Gallatin County, Montana, as well as Long Lake
 2.90 (LL), Mitchell Lake (ML), and the Niwot Ridge Long Term
 Ecological Research site (NWT) in Boulder County, Colorado.
 Sampling occurred during summer 2010–2013 at most sites
 except SC, which was only sampled in 2013, and EL which
 was sampled in 2009–2012 but not sampled in 2013 (due to
 2.95 a forest fire). Pikas were livetrapped and sampled under light
 anesthesia (inhalant anesthetic, Isoflurane) during a 20-min
 handling process. Live animal research followed guidelines
 of the American Society of Mammalogists (Sikes et al. 2011)
 under trapping and sampling protocol 1104.06, approved by
 2.100 the University of Colorado-Boulder Institutional Animal Care
 and Use Committee. Research permits were obtained from
 Montana Fish, Wildlife and Parks (2010-064), Colorado Parks
 and Wildlife (TR2014), and the United States Forest Service
 (BOU390). Individuals were marked with unique, color-coded
 2.105 ear tags and released at point of capture. Sex and age class
 (adult or juvenile) were determined visually, and physiologi-
 cal data for each individual were collected, including weight,
 rectal body temperature, cover class of parasitic mites on the
 outer ear (none, low, medium, and high corresponded to 0, < 4,
 2.110 < 16, and > 16 mm², respectively), and number of fleas observed
 dropping from the fur in response to anesthesia. Additionally,
 2.112

the microhabitat associated with each marked pika was characterized in terms of variables that influence microclimate (elevation, slope aspect). By design, our study sites were dominated by either north-facing or south-facing slopes and high or low elevations, and trapping locations were preselected to represent these classes of elevation and aspect. We conducted annual resights according to a robust design (Kendall et al. 1995), with 2–6 resight attempts per individual during August and September of each year through 2014. Each survey involved 1 or more observers noting the ear tags of all surface-active pikas during a 20-min point-survey of the territory of a previously tagged pika and all adjacent territories. In most cases, a single observer could view several territories from a single vantage point. In this manner, all territories within 1 km of each capture were surveyed 2–6 times each summer. Pikas are highly philopatric and adults rarely disperse distances greater than 1 km after territory establishment (Smith and Weston 1990; Peacock 1997). Typically, adult individuals disappear from the population due to mortality rather than dispersal, as evidenced by low immigration into fully marked populations (Smith and Ivins 1983, 1984). Pika detection probability has been reported as high (> 90%) consistently across studies throughout the western United States (Beever et al. 2008; Beever et al. 2010; Rodhouse et al. 2010; Erb et al. 2011; Moyer-Horner et al. 2012; Jeffress et al. 2013; Ray et al., in press). Thus, a marked pika was classified as nonsurviving when we failed to relocate it.

Blood and fecal samples were obtained at a range of times after initial capture as a result of our field protocol (traps were checked at approximately 2-h intervals and trapped pikas were handled in the order they were discovered). It was not feasible to determine initial time of capture because we could not observe traps directly without eliminating trap success; traps were buried in the talus to improve trapping success and pika survival. The range of sampling times (20–180 min after initial capture) ensured that our GC samples represented an acute stress response to captivity and handling, rather than baseline GC, which must be measured within 3 min of initial capture (Touma and Palme 2005). We were not able to collect blood samples within 3 min of capture due to the time required for trap retrieval and anesthesia prior to sampling. GCM samples represented baseline levels, however, because fecal samples would not reflect a GC response until 10–12 h after initial capture (Wilkening et al. 2013). Blood was collected via retro-orbital bleeding, and samples were separated into plasma on-site using a portable centrifuge. Fecal samples were collected when produced during handling. Pikas produce 2 types of feces: cecal feces, which are commonly reingested, and fecal pellets, which are not reingested. Previous analyses identified significant differences in GCM concentration between the 2 types of feces (Wilkening et al. 2013). Only fecal pellets were analyzed here because the majority of samples were of this type. All samples were held on ice in the field and stored at –20°C in the laboratory.

Sample analysis.—Comparative analysis of GC and GCM concentration in samples was done using a Correlate-EIA Corticosterone Enzyme Immunoassay Kit (Arbor Assay Design,

Inc., Ann Arbor, Michigan; cat. no. K014-H1). Extraction and analysis protocols followed those established by Arbor Assays, Inc., which were validated specifically for pikas by Wilkening et al. (2013). Plasma samples were first diluted with an equal volume of the supplied Dissociation Reagent, then diluted further with the supplied Assay Buffer prior to assay. Fecal samples were lyophilized and ground into powder using a mortar and pestle. A portion of the total dried fecal material sample (0.100 g) was blended with 1 ml of 90% aqueous ethanol using a vortex shaker (Vortex Genie 2; Scientific Industries, Inc., Bohemia, New York). Samples were then centrifuged at 5,000 revolution/min for 15 min, and the resulting supernatant was drawn off and transferred to a clean tube for evaporation. The supernatant solution was evaporated to dryness in a vacuum centrifuge and extracts were stored at –20°C. Immediately prior to the assay, fecal sample extracts were reconstituted with a mixture of ethanol and assay buffer and were mixed completely using a vortex shaker.

During each assay, samples were analyzed in triplicate alongside a standard curve of 7 known concentrations of corticosterone (5,000, 2,500, 1,250, 625, 312.50, 156.25, 78.125 pg/ml). Values for each extracted sample were generated using a microplate reader (BioTek Microplate Reader Synergy HT; 2005 Biotek Industries, Inc., Winooski, Vermont) and Gen 5 1.11 Data Analysis software. Intra-assay coefficients of variation were less than 10% and inter-assay coefficients of variation were less than 15%. Final concentrations of plasma GC were expressed as pg/ml, and fecal GCM were expressed as pg/g.

Data analysis.—Juveniles were omitted from analyses, due to significant differences between juveniles and adults in both GC and GCM concentration (Wilkening et al. 2013), and because juvenile dispersal events could be mistaken for mortality. Adult resight histories suggested very high detection probability (see “Results”). Therefore, the annual adult survival rate for each year t and site x was calculated as $S_{t,x} = N_{t+1,x} / N_{t,x}$, where $N_{t,x}$ was the total number of adults tagged and sampled for GC/GCM during the year t at site x . Survival for 2 or more years after GC/GCM sampling was not considered in the current analysis, because most pikas were sampled only once. F -tests were used to assess the equality of variances between sample populations in order to determine the appropriate t -test, and either Student’s parametric or Welch’s nonparametric t -test was used to identify differences in either GC or GCM concentration between sexes and between individuals that survived and those that did not. Prior to analysis, data were checked for outliers, normal probability plots were examined, and a Shapiro–Wilks statistic was calculated to test for normality. Several predictors (GC, GCM, number of fleas observed) were log transformed to correct for observed heteroscedasticity. All statistical analyses were conducted using R 3.0.1 (R Core Team 2013) and significance was assessed at the $\alpha = 0.05$ level.

Survival models.—For models of survival during the year after sampling, candidate predictor variables represented physiological metrics shown to influence survival in other species (Arnold and Anja 1993; Brown et al. 1995; Vander Haegen 2013), and habitat characteristics identified as predictive in

previous studies of the pika (Rodhouse et al. 2010; Jeffress et al. 2013). Physiological metrics included GC and GCM concentration, body weight, and ectoparasite abundance (number of fleas observed and cover of ear mites). Habitat characteristics included elevation classed as low, medium, and high with respect to latitude- and longitude-adjusted values for pikas (Hafner 1993) and the aspect of the slope of an individual's territory. Site (EL, NWT, LL, ML, SC), year (2009–2013), sex (male or female), and state (Colorado or Montana) were also included as predictors, to account for any differences due to these factors. Potential predictors of survival were abbreviated as: GC (GC concentration measured in blood samples); GCM (GCM concentration measured in fecal samples); Wt (body weight); Mite (ear mite coverage); Flea (number of fleas observed); Elev (elevation); Asp (slope aspect).

Survival during the year after sampling was used as the response variable in logistic regression models. Relative support for each predictor variable was evaluated using models with all possible combinations of predictors, but the relative support for each model was evaluated only for models which did not include highly correlated predictors (Spearman's $P > 0.5$). An interaction term was included for every combination of predictors in the model. Interaction terms were omitted if far from significant (P value > 0.10). Our data set included GC or GCM measurements for all individuals ($N = 109$), and both GC and GCM for a subset of individuals ($N = 59$). To retain the largest sample size and maximize the number of models considered, 2 different model sets were used to examine survival: "GC models" included all individuals sampled successfully for GC ($N = 89$) and "GCM models" included all individuals sampled successfully for GCM ($N = 79$). The relative support for each model was calculated separately for each model set using ~~corrected~~ Akaike information criterion (AIC_c) (Burnham and Anderson 2002). We assumed that models with similar levels of support would differ in AIC_c by less than 2 points, models with disparate levels of support would differ by more than 4 points, and the model with best support would have the lowest AIC_c score within the model set (GC or GCM). Model averaging and the ranking of predictor variables were performed using the R package MuMIn (Barton 2014), which ranks predictors based on Akaike weights. Ranking predictors requires a relatively full model set in which each predictor appears in a similar number of models. For this analysis, we focused only on the subset of pikas for which both GC and GCM were measured ($N = 59$). Using these data, we constructed a global model including all predictors described above, with no interaction effects, and used MuMIn to rank each predictor based on Akaike weights for this global model and all subsets.

RESULTS

Survival rate.—Resight data from repeated observations indicated a high probability (> 0.9) of detecting surviving pikas, similar to the high probability of detecting habitat patch occupancy (also > 0.9) in other pika studies (Rodhouse et al. 2010; Jeffress et al. 2013). For a given pika, there were no instances

of nondetection followed by detection, or detection followed by nondetection, among repeated surveys within a summer. Survival for 1 year after sampling among adult pikas sampled for GC or GCM was highest every year in Montana, and consistently lower at sites in Colorado (NWT, LL, ML; Table 1). However, the difference between annual Montana and annual Colorado survival rates 2010–2013 was only marginally significant in a paired t -test ($t = 2.480$, $d.f. = 3$, P value = 0.089). The lowest annual survival rate in 2010 and 2013 was at LL, and the lowest annual survival rate in 2011 and 2012 was at ML. In Montana, annual survival rate was highest in 2012 (EL) and lowest in 2009 (EL). Among Colorado sites, annual survival was lowest during 2010 at NWT and LL, and at ML it was lowest during 2012. Among Colorado sites, the highest rate of annual survival was recorded during 2011 at NWT and LL, and during 2013 at ML (Table 1).

Relating survival to GC and GCM.—GC concentration was significantly higher in males than in females (Welch's t -test, $t(38.22) = -3.02$, P value < 0.001), so additional tests examining survival and GC concentration were split by sex. Among males, mean GC concentration was higher in pikas that survived for 1 year after sampling (735.62 pg/ml) than those that did not (551.24 pg/ml), although this difference was not significant (Welch's t -test, $t(33.57) = -1.08$, P value = 0.29). Mean GC concentration was roughly the same among females that survived (373.57 pg/ml) and those that did not (379.58 pg/ml). There was no difference in mean GCM concentration between males (3501.43 pg/g) and females (3438.84 pg/g; Welch's t -test, $t(72.51) = -0.10$, P value = 0.92). Mean GCM concentration was significantly lower in individuals that survived (2176.95 pg/g) than in those that did not (5352.88 pg/g; Welch's t -test, $t(34.8) = 4.75$, P value < 0.001 ; Figure 1).

Survival models.—Among predictor variables used in GC models (models of survival based on pikas sampled for GC), elevation was positively correlated with weight (Spearman's $P = 0.54$) and number of fleas observed (0.53), and negatively correlated with ear mite cover (-0.66). Ear mite coverage was also negatively correlated with weight (-0.51) and number of fleas observed (-0.62), while weight was positively correlated with number of fleas observed (0.53). Correlations among all other predictor variables in this model set were < 0.22 . GC models were constructed using all combinations of predictors

Table 1.—Annual survival rate estimated for adult pikas (*Ochotona princeps*) included in this study at 4 sites in the Rocky Mountains. Sample size is given in parentheses and indicates the number of individuals that were marked and sampled in that particular year. EL = Emerald Lake; LL = Long Lake; ML = Mitchell Lake; NA = not available; NWT = Niwot; SC = Swan Creek.

Year	Montana		Colorado		
	EL	SC	NWT	LL	ML
2009	0.67 (3)	NA	NA	NA	NA
2010	0.78 (9)	NA	0.40 (5)	0.00 (4)	0.40 (5)
2011	0.73 (11)	NA	0.63 (19)	0.86 (7)	0.50 (4)
2012	0.90 (10)	NA	0.50 (8)	0.67 (6)	0.14 (7)
2013	NA	0.71 (7)	0.60 (10)	0.50 (4)	0.75 (4)

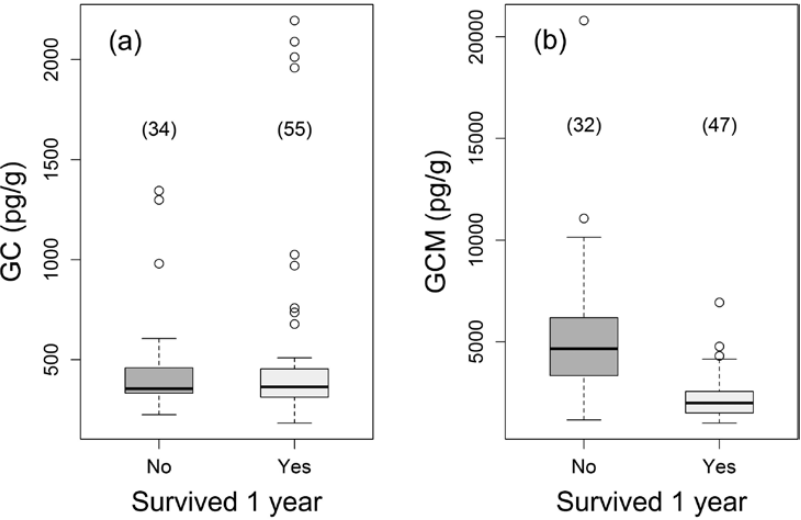


Figure 1.—Stress metrics versus survival. Our metric of acute stress, a) plasma GC, was not related to survival, but our metric of chronic stress, b) fecal GCM, was much higher in pikas (*Ochotona princeps*) that did not survive the year following capture (Welch’s *t*-test, $t(34.8) = 4.75$, P value < 0.001). Sample sizes (shown in graphs) differed between (a) and (b) because we were not able to sample both GC and GCM from every pika. GC = glucocorticoid; GCM = glucocorticoid metabolite.

with low pairwise correlations (< 0.5). Physiological metrics that appeared in well-supported models of survival included body weight (positive effect), ear mite coverage (negative effect), and number of fleas observed (negative effect). Site was also a predictor in all models with good support ($\Delta AIC_c < 2$) with aspect appearing in one of those models (Table 2).

Among predictor variables used in GCM models (models of survival based on pikas sampled for GCM), elevation was positively correlated with number of fleas observed (0.53), and negatively correlated with ear mite coverage (-0.52). Ear mite coverage was also negatively correlated with number of fleas observed (-0.54). Correlations among all other predictor variables in this model set were < 0.19 . GCM models were constructed using all combinations of predictors with low pairwise correlations (< 0.5). In this analysis, the best model included GCM and number of fleas observed as predictors, which were both negatively correlated with survival (Table 3; Figure 2). Sex also appeared in the 2 models with similarly high support ($\Delta AIC_c < 2$), with males/females having lower survival. GCM concentration appeared in all supported models in this set ($\Delta AIC_c < 4$; Table 3). State received less overall support as a predictor of survival. No interaction terms were significant, and all interactions were omitted from the final models. Among predictors of pika survival, a negative effect of GCM garnered most support (Akaike weight = 0.88), followed by a negative effect of number of fleas observed (0.79; Table 4).

DISCUSSION

In order to better understand wildlife population dynamics, we need information related to key factors affecting patterns and rates of individual survival. This is particularly imperative for a species in decline, such as the American pika, which has been considered for listing as threatened or endangered. However, vulnerable wildlife species are often those most difficult to

Table 2.—Relative support for survival models based on pikas (*Ochotona princeps*) sampled for GC concentration at Rocky Mountain sites. Models are ranked in order of increasing AIC_c (Akaike’s information criterion). ΔAIC_c is the difference between the indicated model and the best model (lowest AIC_c). Only well-supported models ($\Delta AIC_c < 4$) are shown, except for the Null model. GC = glucocorticoid. Asp = slope aspect; Flea = number of fleas observed; Mite = ear mite coverage; Wt = body weight.

Model	AIC_c	ΔAIC_c
Wt + Site	112.95	
Site	113.27	0.32
Flea + Site	114.43	1.48
GC + Asp + Site	114.47	1.52
GC + Wt + Site	114.52	1.57
GC + Site	114.82	1.87
Mite + Site	115.2	2.25
State	116.4	3.45
GC + Mite + Site	116.75	3.80
Null	120.38	7.43

locate or capture, and collecting demographic data can be challenging. The numerous noninvasive or minimally invasive sampling techniques which have been developed recently to assess the endocrine condition of an animal are being used increasingly in wildlife conservation research (Cockrem 2005; Heath and Frederick 2005; Wikelski and Cooke 2006). Information gleaned from endocrinology tools provide invaluable insight regarding the current physiological condition of an animal, but interpretation of results can be complicated. Given that increases in GCs sometimes predict mortality and decreased reproduction, one would expect that higher GCs indicate stress. But research has shown that GCs do not always change in a predictable pattern in response to unfavorable conditions (Breuner et al. 2008), and that the relationship between GCs and survival or reproductive success is often nonlinear (Busch and Hayward 2009). Some of this variation may be explained by

Table 3.—Relative support for survival models based on pikas (*Ochotona princeps*) sampled for GCM concentration at Rocky Mountain sites. Models are ranked in order of increasing AIC_c (Akaike’s information criterion). ΔAIC_c is the difference between the indicated model and the best model (lowest AIC_c). Only well-supported models (ΔAIC_c < 4) are shown, except for the Null model. GCM = glucocorticoid metabolite. Asp = slope aspect; Elev = elevation; Flea = number of fleas observed; Mite = ear mite coverage; Wt = body weight.

Model	AIC _c	ΔAIC _c
GCM + Flea	72.92	
GCM + Flea + Sex	73.36	0.44
GCM	74.32	1.40
GCM + Sex	75.01	2.09
GCM + Year	75.32	2.40
GCM + State	75.32	2.40
GCM + Wt	75.43	2.51
GCM + Elev	76.26	3.34
GCM + Mite	76.28	3.36
GCM + Asp	76.30	3.38
Null	112.53	39.61

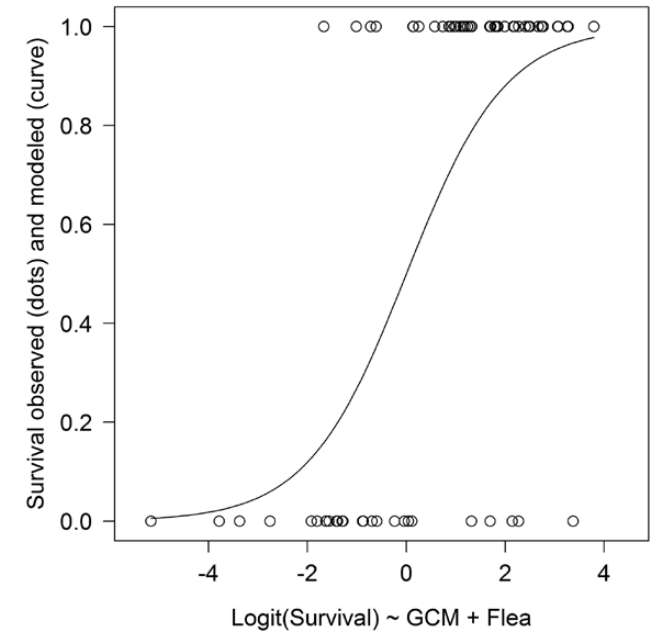


Figure 2.—Observed survival and modeled probability of survival of pikas (*Ochotona princeps*) in the Rocky Mountains. The best model of survival (ΔAIC_c = 0; Survival ~ GCM + Flea) is shown here. AIC = Akaike’s information criterion; GCM = glucocorticoid metabolite.

differences in sampling or analysis methodologies, but there might also be a physiological basis for these inconsistencies. There are a variety of instances in which high GCs could positively correlate with survival, such as the energetic demands associated with migration, escape from predators, or reproductive effort. For example, studies of bird species have asserted that sustained, elevated GCs are necessary in order to generate the energy required for successful reproduction (Beletsky et al. 1989; Love et al. 2004; Bortolotti et al. 2008). Individuals may be in good physical condition and thus more likely to survive, but may still maintain high GCs for extended periods of time

Table 4.—Relative support for predictors of pika (*Ochotona princeps*) survival. Akaike weights were calculated across all possible models using data from individuals for which we measured both GC and GCM (*N* = 59). Each model included only direct effects based on 1–11 of the 11 predictor variables. GC = glucocorticoid; GCM = glucocorticoid metabolite. Asp = slope aspect; Elev = elevation; Flea = number of fleas observed; Mite = ear mite coverage; Wt = body weight.

Predictor	Akaike weight
GCM	0.88
Flea	0.79
Site	0.55
State	0.51
Elev	0.38
Year	0.29
Asp	0.29
Sex	0.23
Wt	0.23
GC	0.22
Mite	0.09

while raising offspring. This could lead to positive relationships between GCs and metrics of fitness, such as survival and reproductive success, especially when sampling occurs during or immediately after the breeding season. Factors related to the life-history characteristics of the species should always be considered when examining relationships between fitness and metrics of stress. Therefore, it is important to identify which endocrine metrics are the most informative for a species, given the limited time and resources that characterize many wildlife conservation research projects.

Here, our results indicated that GCM concentration was the strongest predictor of annual survival in pikas, suggesting that individuals with higher baseline GCM concentration may be less likely to survive (Figure 1). Among commonly used endocrine metrics, those measuring baseline GCM concentration are the most readily related to survival, since this metric reflects the allostatic load of the individual and may be indicative of chronic stress. There is support for the expected negative relationship between high baseline GCM concentration and survival in the literature (Busch and Hayward 2009), although studies pertaining to lagomorph species are rare. Research related to pygmy rabbits (*Brachylagus idahoensis*) has shown that higher GCM concentration measured in adult females was related to reduced reproduction and survival of subsequent litters (Scarlata et al. 2012). However, another study on captive European rabbits (*Oryctolagus cuniculus*) found that higher GCM concentration was positively associated with survival and negatively associated with body condition (Tablado et al. 2012). In this case, rabbits were kept in captivity for 2–4 weeks and then reintroduced into a new area. Measurements collected during the captivity period most likely reflect the stress response of individuals, rather than an accurate measurement of chronic stress. This interpretation was corroborated by the fact that higher plasma GC concentration was also positively related to survival, and these measurements were not considered baseline (Tablado et al. 2012). Examples such as this illustrate the importance of standardized definitions of baseline measurements and chronic stress. In our study, GCM samples were collected from

free-ranging individuals, and capture-associated stress was not reflected in fecal samples because they were collected within 3 h of initial capture, too soon to allow for excretion of metabolites resulting from elevated GCs (Wilkening et al. 2013). Our hypothesis that survival would be higher for individuals with lower levels of chronic physiological stress, as indicated by lower GCM, was well supported by our results.

Contrary to our other hypothesis that survival would be higher for pikas with higher GC, we did not find a significant positive relationship between GC concentration and survival. This metric was considered an acute stress response in our study, rather than a baseline measurement, given that we were measuring how an individual responded to capture stress more than 3 min after capture. Other studies have documented increased GC concentration in vertebrates in response to a stressor, but many fail to take into consideration how the natural variability in GC concentration relates to fitness. A recent review examining studies related to the acute stress response and 2 metrics of fitness (survival and reproduction) found that survival could be predicted (nonlinearly) by high or low GC concentration, and that the direction of the relationship was often confounded by the reproductive state of the individual (Breuner et al. 2008). Busch and Hayward (2009) offer a modified log-quadratic relationship between survival, reproduction, and measures of stress to explain inconsistencies across studies. They suggest that baseline GCs (plasma or fecal) need to be high enough to support the extra physiological demands of reproduction, but not so high as to disrupt required behavioral processes. Similarly, an acute stress response should protect the individual from dying in the pursuit of reproduction but should not always favor individual survival over survival of young (Busch and Hayward 2009). When placed in the context of survival and reproduction, high GCs are not always detrimental. We did not consider the reproductive status of individuals because reproductive status was often unknown, and this may help to explain the lack of a relationship between GC and survival. Additional information related to reproductive status in pikas could help to clarify the relationship between GCs and survival, and future studies could examine a log-quadratic relationship between survival, reproduction, and stress for this species.

It is worth noting that our model of pika survival as a function of GCM and flea load appears to have higher sensitivity than specificity. That is, it may be more accurate in predicting cases of survival than cases of mortality. This pattern likely derives from the diversity of sources of mortality for small mammals, and the relative importance of health in survival. Our model would likely underpredict mortality unless the threshold for prediction was raised, relative to the threshold for prediction of survival.

We also found that pika survival was negatively related to the number of fleas measured on an individual, which supported our hypothesis that survival would be higher for individuals with fewer ectoparasites. A higher number of fleas may indicate individuals in poor health that are less likely to survive (Devevey and Christie 2009) or could identify individuals more susceptible to mortality as a result of diseases transmitted through

fleas (Collinge and Ray 2006). Little is known about disease and pikas, although past studies have revealed that pikas harbor 66 species of ectoparasites (Severaid 1955). Fleas can carry plague, which has been detected in pikas in Mongolia (Galdan et al. 2010), and plague could play a role in pika extirpations in the United States (Biggins and Kosoy 2001). Relationships between survival and fleas have been identified in other mammals, such as prairie dogs, which are more likely to survive in colonies subject to flea-control treatments (Biggins et al. 2010). Our results suggest that pika survival could be negatively impacted by disease transmitted via fleas. Future studies could incorporate protocols designed to detect pathogens in fleas.

Our final hypothesis, that survival would be higher for individuals living in microhabitats characterized as more suitable in previous studies, was not supported by our results. Microclimatic influences considered here were not predictive of annual survival. However, only broad classes of elevation and aspect were considered as proxies for the processes generating microclimate. The lack of support for elevation and aspect as predictors of pika survival could be due to our rough scheme of classification for these variables, which were placed into broad categories, rather than measured with precision. Although many studies have predicted pika occupancy patterns using topographical proxies, specific data on microclimate have also predicted patterns of pika occupancy and persistence in the Great Basin (Beever et al. 2010, 2011; Wilkening et al. 2011) and in the Northern Rockies (Yandow et al. 2015). Future studies could incorporate specific measurements of microclimate (e.g., temperature data), and incorporating comparisons between survival and GCs across regions that vary climatically would be particularly informative.

One factor not examined in our study was predator abundance, which has been shown to positively correlate with both baseline and stress-induced GC measurements. Individuals can experience chronic stress in response to sustained, high levels of predation (Boonstra et al. 1998; Scheuerlein et al. 2001; Clinchy et al. 2004) and also rely on an elevated acute stress response as a means of escape (Mateo 2007). High poaching pressure is positively related to GCM concentration measured in African elephants (*Loxodonta africana*—Gobush et al. 2008) and direct chase by humans evokes a stress response in red deer (*Cervus elaphus*) and ocean fish (Bateson and Bradshaw 1997; Galima et al. 2005). Pikas are preyed upon by weasels (Smith and Weston 1990) and it is likely that predation pressure influences both survival and GC response in pikas. Future studies could incorporate measurements estimating local predator density or abundance. Additional factors shown to influence GC measurements in other species include diet (von der Ohe et al. 2004; Thiel et al. 2011; Stetz et al. 2013) and genetic variation (Sapolsky et al. 2000). Dietary fiber may affect fecal mass, gut passage time, or gut microbial activities, which could alter GCM concentration (von der Ohe and Servheen 2002). Genetic variation was a likely factor in our study, which included 2 subspecies (*O. p. princeps* and *O. p. saxatilis*) from 2 different states (Montana and Colorado, respectively). The perception of a stressor and the resulting release of stress hormones (GCs) is

adaptive, and therefore the relationship between survival and GCs may be influenced by genetics. These factors should be examined as predictors of stress and survival in future studies.

- 8.5 Ultimately, identifying factors that cause stress in pikas, as indicated by GC measurements, may allow us to alleviate negative stressors contributing to population decline and increase the chance of survival. Pika populations appear to be declining in some regions and continued range contraction may occur as a result of climate change. Techniques established here can be used in future studies to determine whether local habitat variables related to climate can explain levels of physiological stress and rates of survival for individuals. If local variables related to climate can explain stress and survival, then climate change may have relatively direct effects that are contributing to local extinctions of this species. Otherwise, local extinctions may be related to climate change only indirectly (e.g., through the redistribution of disease agents) or to other changing factors (e.g., human land use patterns). Increased understanding of these relationships will allow for better prediction of potential climate change impacts and can aid in management and conservation efforts for this iconic species.

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