

Severe Drought Impacts Female Pheasant Physiology in Southwest Nebraska

JESSICA A. LASKOWSKI*, GWEN C. BACHMAN, AND JOSEPH J. FONTAINE

Nebraska Cooperative Fish and Wildlife Research Unit, School of Natural Resources,
University of Nebraska-Lincoln, Lincoln, NE 68583 USA (JAL)

School of Biological Sciences, University of Nebraska, Lincoln, NE 68588 USA (GCB)

U.S. Geological Survey, Nebraska Fish and Wildlife Research Unit, School of Natural Resources,
University of Nebraska-Lincoln, Lincoln, NE 68583 USA (JJF)

*Corresponding author: jlaskowski@ufl.edu

ABSTRACT In 2012, Nebraska experienced one of the worst droughts since the 1930s, accompanied by abnormally high temperatures. We studied the impacts of the 2012 summer drought on female ring-necked pheasant (*Phasianus colchicus*) body condition and baseline and stress-induced corticosterone concentrations (CORT). We hypothesized that drought conditions would reduce pheasant body condition, increase chronic stress resulting in elevated baseline CORT levels, and down-regulate pheasant stress response to acute stressors, resulting in reduced stress-induced CORT concentrations. In southwestern Nebraska, we captured female pheasants in 2012 (pre-drought) and 2013 (post-drought). Pheasants had poorer body condition after the drought. Although female CORT measures were similar among years (baseline: $F_{1,8} = 0.591$, $P = 0.465$; stress-induced: $F_{1,26} = 1.118$, $P = 0.300$), females in poorer condition had elevated baseline CORT ($F_{1,26} = 6.446$, $P = 0.018$) and stress-induced CORT ($F_{1,26} = 8.770$, $P = 0.006$) with potential negative consequences for reproduction. Our results suggest that it is critical for managers to consider how to buffer the negative impacts of drought on pheasant physiology and population growth, as droughts are likely to occur more frequently in southwest Nebraska in the next century.

KEY WORDS body condition, corticosterone, drought, Great Plains, *Phasianus colchicus*, ring-necked pheasants.

Climate change is predicted to increase surface air temperatures at a rate that is likely to exceed the ability of some species to adapt (Thomas et al. 2004, Jump and Penuelas 2005, Garnier and Lewis 2016). Efforts to understand the implications for wildlife of a warmer planet are largely focused on identifying species-specific climate envelopes, but changes in the rate of extreme climatic events such as drought are an equally impactful and increasingly apparent outcome of climate change (Jentsch et al. 2007, Albright et al. 2009). For example, in southwest Nebraska, USA, surface air temperature is projected to increase 2–5° C by the end of the century, leading to a reduction in soil moisture and increasing the likelihood and potential severity of droughts (Shafer et al. 2014, Walsh et al. 2014). Therefore, a better understanding of how extreme climate events (e.g., drought) affect wildlife species is needed to develop strategies to mitigate the potential implications of climate change for wildlife populations.

In 2012, the Great Plains experienced one of the most severe seasonal droughts in 117 years (Hoerling et al. 2014). Rainfall, which primarily occurs from May through August, was approximately two standard deviations below average (Hoerling et al. 2014). Moreover, the summer of 2012 was the third warmest since the 1930s (Mallya et al. 2013). The combination of low rainfall and high temperatures resembled the Dust Bowl era of the 1930s (Mallya et al. 2013, Hoerling et al. 2014), creating conditions which

simultaneously increased the water requirements of wildlife while reducing water availability on the landscape (Ji and Peters 2003, Johnson et al. 2011). Conditions during the 2012 drought led to a 20–60% reduction in grassland productivity, corresponded with the lowest corn yields in nearly 20 years, and 59% of the rangelands exhibiting poor condition (Knapp et al. 2015, Rippey 2015). For wildlife, the consequences of the 2012 drought were in some cases extreme. For example, populations of ring-necked pheasant (*Phasianus colchicus*; hereinafter pheasant) in Kansas declined by nearly 40% from 2012 to 2013 (Dahlgren 2013).

The pheasant is an iconic species that like most grassland birds, shows long-term population declines (Suchy et al. 1991, Dahlgren 1998). Pheasant population declines have contributed to declines in hunting license sales, which fund conservation efforts for game and non-game species (Suchy et al. 1991, Dahlgren 1998). While there is considerable effort to reverse pheasant population declines (Rogers 2002), it remains unknown how changing climatic conditions, such as increases in drought frequency, may affect pheasant populations and thus management success. For many bird species, drought causes population declines due to low reproductive success in combination with low survival rates (Christman 2002, Mooij et al. 2002, Albright et al. 2009). As drought is predicted to become more frequent and extreme in the Great Plains, it is critical to understand the underlying mechanisms that may shape how drought influences population dynamics to develop

approaches to mitigate climate change impacts (Alley et al. 2003).

During drought, environmental stressors can take a physiological toll on individuals as food and water resources decline. Resource limitation can have cascading effects by not only affecting body condition, but by altering physiology (Sapolsky et al. 2000). Avian responses to food or water stress include the activation of the hypothalamus-pituitary-adrenal axis and the corresponding release of corticosterone (hereafter CORT), the main stress hormone in birds (Siegel 1980). Increased plasma CORT concentrations initiate the mobilization of energy reserves by temporarily pulling resources from non-essential bodily functions (e.g., immune function, reproduction; Sapolsky et al. 2000, Romero 2004), and shunting energy reserves to support activities that mediate environmental stressors (e.g., hyperphagia, anti-predator behaviors; Wingfield et al. 1998). Corticosterone is released in response to chronic and acute stressors. Baseline CORT levels reflect conditions that animals experience for long periods in the absence of acute stressors (Romero 2002). Stress-induced CORT levels represent short-term plastic responses to acute environmental perturbations (Wingfield 2013). Chronically elevated CORT concentrations (baseline and stress-induced) can have deleterious effects including impaired cognitive abilities and immune function (Wingfield et al. 1998, Wingfield and Sapolsky 2003). During the breeding season, elevated CORT concentrations can reduce reproductive success and even cause females to forego breeding entirely (Sapolsky et al. 2000).

We assessed female pheasant body condition as well as baseline and stress-induced CORT before and after the 2012 summer drought in southwestern Nebraska. We studied females exclusively because pheasant population growth largely depends upon female survival and reproductive success, as multiple females breed with one male (Clark et al. 2008). First, we hypothesized that drought conditions would reduce pheasant body condition due to a decline in food and water availability. Second, we hypothesized that drought conditions would increase chronic stress resulting in elevated baseline CORT levels due to reduced food intake and increased perceived predation risk (due to reduced cover; Sapolsky et al. 2000). Last, we hypothesized that pheasants exposed to drought conditions would down-regulate their stress response to acute stressors, resulting in reduced stress-induced CORT concentrations, as maintaining elevated CORT concentrations is costly (Rich and Romero 2005).

STUDY AREA

Our study was conducted in 2012 and 2013 across Hitchcock, Hayes and Red Willow counties in southwestern Nebraska, a semi-arid climate with flat and gently rolling hills interspersed by canyons. Elevation ranges from 650 to 1,000 m (Simonsen and Fontaine 2016). Land use was

dominated by irrigated and dryland crops including corn, soybeans, winter wheat and sorghum. Corn and wheat comprised the majority of crops harvested (on average 52% and 33%, respectively) across Hitchcock, Hayes and Red Willow counties in 2012 and 2013 (NASS 2017). Native rangelands support short-grass prairies. Fields enrolled in the Conservation Reserve Program (CRP) were common and generally comprised of native vegetation such as little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon, gerardii*), Indiangrass (*Sorghastrum nutans*) and a variety of forbs. Our study area consisted of 12 study sites, each a CRP field (30–126 ha) separated by at least 2 km to minimize movement between sites as pheasants generally remain within a 2-km radius home range (Smith et al. 1999).

METHODS

Environmental Conditions

We obtained average monthly precipitation and temperature for 2011 and 2012 from three NOAA weather stations located in McCook, Culbertson and Trenton, Nebraska (NOAA 2016). The three weather stations were approximately equidistant from one another, spanned the extent of our study area from east to west, and were each less than 16 km from the nearest study site. We quantified average monthly precipitation and temperature throughout the fall and winter (September – March) and the spring and summer (April – August) by averaging values across months and weather stations. Average monthly precipitation in spring and summer months (April – August) of 2012 was approximately 35% below historical averages (1981 – 2010; historical spring-summer monthly average precipitation = 7.56 cm, SE = 0.28, 2012 spring/summer monthly average precipitation = 4.87 cm, SE = 0.82; NOAA 2017).

Capture and Handling Techniques

To assess the potential effects of drought on pheasant physiology, we compared individual birds captured before the summer drought (spring 2012) to those captured the year following the drought (spring 2013). We captured female pheasants via night lighting (Labisky 1968) from late February through early April. We extracted blood samples (~150 μ l) from the brachial vein with a 30 gauge needle and heparinized microcapillary tubes within 3 min of capture and 20 min after capture to assess total baseline and ‘stress-induced’ CORT concentrations. We stored blood samples on ice in small coolers for no more than 9 h before being centrifuged. We stored samples at -18° C in the field and subsequently transferred them to within 3 weeks to -80° C storage until analysis. We measured body mass with a 2.7-kg spring scale accurate to 2 g (CCI Scale Co. Inc. model HS-6, Clovis, California, USA) and tarsus length with a digital

caliper accurate to 0.01 mm (Carrera Precisions 0–150mm digital caliper, model CHICO14, Ontario, California, USA). All methods were in accordance with the University of Nebraska-Lincoln Institutional Animal Care and Use Committee (Protocol 1060).

Body Condition and Corticosterone Concentration

To assess potential effects of the 2012 drought on female pheasant body condition, we calculated an index of body condition (M_c) based on a mass index corrected for capture date and tarsus length (Peig and Green 2009). Tarsus length is a reliable indicator of pheasant structural size (Draycott et al. 1998, Tompkins et al. 1999) while mass is often positively correlated with capture date, potentially reflecting an increase in weight gain as animals exit the winter and as females enter the breeding season (Clark 1979). We corrected mass for capture date with the formula: $M_d = M_i [C_o / C_i]^{bOLS}$ where M_i and C_i are the mass and capture date of the individual, C_o is the population mean capture date, and $bOLS$ is the scaling exponent, the slope (Ordinary Least Squares) of the regression of the natural log of mass by the natural log of capture Julian date for all individuals in the population (Peig and Green 2009). Because we were ultimately interested in the relative body condition for a given size, we corrected this new mass estimate against tarsus length following the same procedure using the standardized major axis slope ($M_c = M_d [T_o / T_i]^{bSMA}$; Peig and Green 2009). We measured total baseline and ‘stress-induced’ CORT concentrations in plasma samples ranging from 10 – 46 μ l (average 32 μ l) via Enzyme Immunoassay (Enzo Life Sciences ADI-901-097, Farmingdale, New York, USA; Wada et al. 2007, Schoech et al. 2013). We optimized the protocol by diluting all samples 1:40 and ran all samples in duplicate.

Statistical Analysis

We log-transformed baseline and stress-induced CORT data to meet normality assumptions. We assessed seasonal precipitation among years and the influence of drought conditions on female pheasant physiology using analyses of covariance (ANCOVA) in Program R (package lme4; Bates et al. 2015). Our models assessing the difference in spring-summer and fall-winter precipitation (average monthly precipitation across weather stations in 2 seasons) among years included year and weather stations as factors. Due to variation in spring-summer precipitation between 2011 and 2012, including spring-summer precipitation in our models to assess pheasant physiology produced similar model predictions as including a year effect. Thus, we used a year effect throughout our analyses in lieu of spring-summer precipitation. Our model assessing the influence of year on body condition included year and study site, but because

CORT is sensitive time of day, temperature at capture, and body condition, we added these additional variables to all analysis of CORT. We omitted any non-significant ($P > 0.05$) interaction terms from the models.

RESULTS

Environmental Conditions

Over 70% of annual precipitation occurred in the spring and summers of 2011 and 2012 (average total spring-summer precipitation = 34.73 cm; average total fall-winter precipitation = 9.47 cm). Average monthly spring-summer precipitation was higher ($F_{1,28} = 9.20$, $P = 0.01$) in 2011 ($\bar{x} = 9.03$ cm, SE = 1.03) than in 2012 ($\bar{x} = 4.87$ cm, SE = 0.82; Fig. 1a). However, during the fall-winter months, average monthly precipitation was similar ($F_{1,38} = 1.20$, $P = 0.28$) between years (2011: $\bar{x} = 1.54$ cm, SE = 0.28; 2012: $\bar{x} = 1.17$ cm, SE = 0.04). Average monthly temperature ($^{\circ}$ C) was similar between years during spring-summer (2011: $\bar{x} = 19.68$, SE = 1.65, 2012: $\bar{x} = 22.12$, SE = 1.39; $F_{1,28} = 1.20$, $P = 0.28$), fall-winter (2011: $\bar{x} = 4.17$, SE = 1.61, 2012: $\bar{x} = 6.30$, SE = 1.57; $F_{1,40} = 0.85$, $P = 0.36$) and across the entire year (2011: $\bar{x} = 10.63$, SE = 1.73, 2012: $\bar{x} = 12.90$ C*, SE = 1.69; $F_{1,70} = 0.85$, $P = 0.36$).

Body Condition and Corticosterone Concentration

We calculated body condition of 55 female pheasants, 21 in spring 2012 and 34 in spring 2013. Female mass was positively correlated with capture date ($\beta = 3.08$, SE = 0.68, $F_{1,55} = 20.85$, $P < 0.001$). After correcting mass for capture date, we then corrected the new mass estimate for tarsus size ($\beta = 4.66$, SE = 3.78, $F_{1,55} = 1.52$, $P = 0.22$). Body condition of post-drought female pheasants ($\bar{x} = 877.57$, SE = 30.52) was 20% lower than the pre-drought population ($\bar{x} = 1026.26$, SE = 22.54; $F_{1,13} = 23.74$, $P < 0.001$; Fig. 1b).

We obtained blood samples from 37 female pheasants, 16 in spring 2012 and 21 in spring 2013. Our Immunoassay (Enzo Life Sciences ADI-901-097, Farmingdale, New York, USA) accuracy averaged 0.15 ng/ml (SE = 0.06). We omitted four birds from analysis because either baseline or stress-induced values fell outside the assay’s standard range. Our final analysis includes baseline and stress-induced plasma CORT of 33 female pheasants, 14 in spring 2012 and 19 in spring 2013. Our analysis includes body condition of 31 of the 33 females from which we assessed baseline and stress-induced CORT. Baseline CORT ($F_{1,26} = 6.45$, $P = 0.02$), stress-induced CORT ($F_{1,26} = 8.77$, $P = 0.01$) and stress response ($F_{1,26} = 4.07$, $P = 0.05$) were all negatively correlated with body condition; however, CORT measures did not differ between pre- and post-drought females (baseline: $F_{1,8} = 0.59$, $P = 0.47$; stress-induced: $F_{1,26} = 1.12$, $P = 0.30$; $F_{1,26} = 1.17$,

$P = 0.29$). Corticosterone measures were not significantly influenced by capture time (baseline: $F_{1,26} = 0.01$, $P = 0.94$; stress-induced: $F_{1,26} = 0.81$, $P = 0.38$; stress response: $F_{1,26} = 0.70$, $P = 0.41$) or capture temperature (baseline: $F_{1,11} = 0.62$, $P = 0.45$; stress-induced: $F_{1,26} = 1.60$, $P = 0.22$; stress response: $F_{1,26} = 1.65$, $P = 0.21$).

DISCUSSION

Pheasants were in poorer body condition following the 2012 drought. Body condition is a proxy for important fitness components such as survival as well as current and future reproduction (Breitenbach et al. 1963, Martin 1987, Draycott et al. 1998). While it is intuitive that reduced body condition could influence pheasant population dynamics by reducing adult survival (Snyder 1985, Wilson et al. 1992), body condition does not generally affect survival in galliformes (Robb et al. 1992). Given the life-history strategy of pheasants, a more profound population effect of drought may be a reduction in reproductive investment. A 7–25% reduction in female pheasant body mass, a reduction commensurate with our observed reduction in body condition, can result in a 90% reduction in reproductive effort (Breitenbach et al. 1963). Indeed, female pheasants that were experimentally starved failed to lay the equivalent of one complete clutch, while a control population laid what is the equivalent of seven clutches (Breitenbach et al. 1963). Renesting rates in wild populations are unlikely to exceed three or four attempts (Gates 1966, Dumke and Pils 1979). Still, assuming a reasonable 25% nest success rate (Baskett 1947, Chesness et al. 1968, Gates et al. 1970, Patterson and Best 1996), one nest attempt per year, versus three, corresponds to roughly a 50% reduction in the number of hatchlings, even if we assume a 20% decline in clutch size between attempts (Decker et al. 2012). Thus, it seems reasonable that the consequences of drought that we measured via body condition likely had significant and immediate population ramifications.

Body condition in pheasants, and many other bird species, is generally thought to reflect food limitation (Jordano 1988, Kitaysky et al. 1999, Brown and Sherry 2006). Dry conditions likely reduced the abundance of natural seeds and invertebrates over the course of our study (Blair et al. 2000), but invertebrates comprise a relatively small proportion of the adult pheasant diet which is almost exclusively composed of agricultural grains (e.g., Fried 1940, Hill 1985). Dry conditions reduce agricultural productivity (Mallya et al. 2013), but given the abundance of grain fields in the area it seems unlikely that even significant decreases in per acre productivity of grain fields led to food limitation. Conversely, drought conditions reduce water content of wild and agricultural seeds (Tilman and El Haddi 1992, Blair et al. 2000), and in our case may have led to a reduction in water intake, which in birds, reliably reduces body condition (Bartholomew and Cade 1963). Irrigated crop fields were the

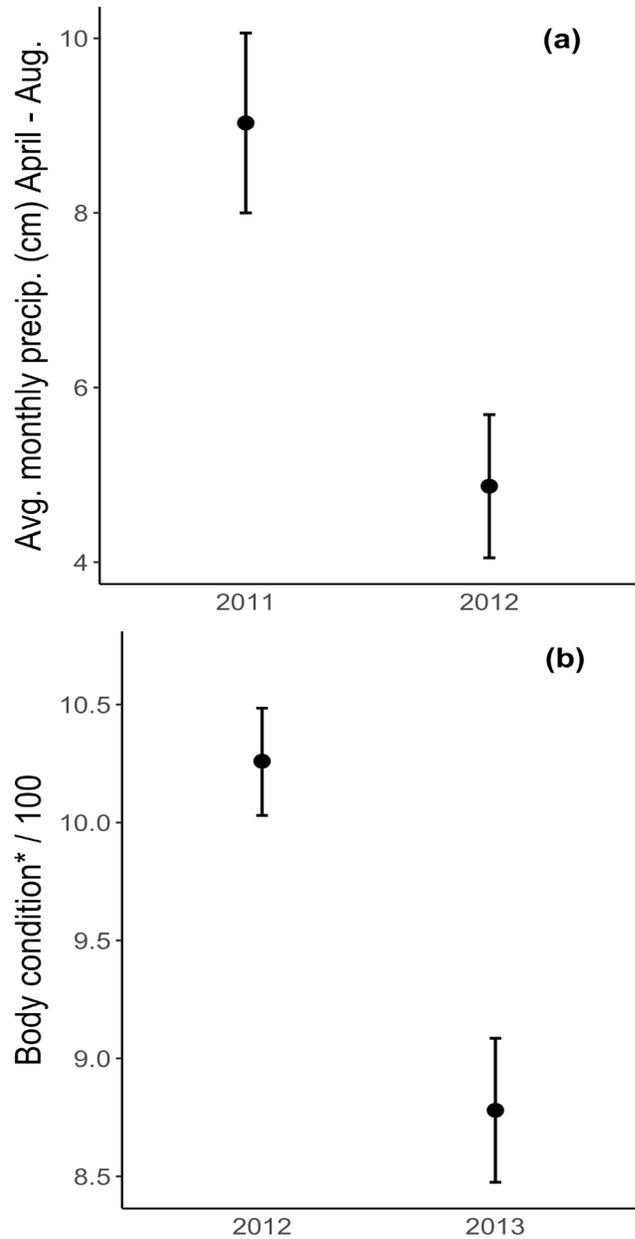


Figure 1. Average monthly precipitation for spring/summer (April – August) in southwestern Nebraska, USA, 2011–2012 (a). Female ring-necked pheasant body condition (measured February through April) in southwestern Nebraska, USA, 2012–2013 (b). Error bars represent standard error. *Body condition was calculated by correcting mass for capture date using the formula: $M_d = M_i [C_o/C_i]^b$ OLS where M_i and C_i are the mass and capture date of the individual, C_o is the population mean capture date and b , the slope of the regression of $\ln(\text{mass})$ by $\ln(\text{capture Julian date})$ for all individuals in the population. The calculation was repeated in order to correct the newly calculated mass by tarsus length ($M_c = M_d [T_o/T_i]^b$ SMA; Peig and Green 2009).

most substantial and reliable water source available in the study area, but were often located outside the home range of most females, highlighting the dependence of pheasants on food resources as source of water. It is unclear whether food or water limitation, or some interaction between them, was the ultimate factor constraining female body condition.

While we failed to find a difference between pre- and post-drought females in any measure of CORT, we did find that females in poorer condition had elevated baseline CORT levels, similar to other studies (Kitaysky et al. 1999, Romero and Wikelski 2001, Williams et al. 2008). Contrary to our hypothesis that drought would lead to a reduced acute stress response, females in poorer condition because of the drought had increased stress-induced CORT concentrations and a larger stress response. Combined with our finding that females failed to regain condition following the drought, our results support the notion that female pheasants in poor condition were possibly exhibiting an 'emergency life history stage'. In this physiological state, individuals mobilize energy reserves to promote behaviors that increase survival and reduce investment in other fitness enhancing activities (e.g., reproduction, territorial and social behaviors; Wingfield et al. 1998). Additionally, in the absence of water or food resources to recover lost condition, elevated CORT concentrations may have exacerbated body condition declines (Sapolsky et al. 2000, Romero 2004).

We failed to find a correlation between drought and CORT and cannot exclude the possibility that CORT is not the mechanistic means by which pheasants deal with largescale environmental perturbation such as drought. However, this seems unlikely as our correlations between body condition and drought, and body condition and CORT suggest that the three phenomena are linked. It is possible that the linkage is time sensitive, such that individuals elevate CORT in response to the immediate onset of the drought, but by the time we measured the response the following spring, CORT levels had declined. Although this would be unexpected when sampling the same individual over time, as we would not expect CORT levels to decline if body condition remained poor (Sapolsky et al. 2000), our samples before and after the drought reflect different individuals and possibly different populations. Pheasants have low annual survival (Snyder 1985, Petersen et al. 1988, Leif 1994), thus it may be that the apparent disconnect between CORT and drought reflects a selection event such that individuals that survive a drought do not have as drastic of a CORT response to the same body condition. Although we hypothesized that drought conditions would down-regulate the acute stress response given the costs of maintaining elevated CORT levels (Rich and Romero 2005), there may be an adaptive advantage to individuals that have a limited CORT response when faced with chronically challenging environmental conditions.

The most parsimonious explanation for our failure to find a link between CORT and extreme drought may

simply be a lack of sampling. Corticosterone levels are responsive to a wide array of environmental conditions, from food availability to predation risk (Wingfield 2013). While ostensibly every individual we observed in 2013 experienced the largescale effects of drought in 2012, localized environmental differences in habitat conditions or predation risk may have masked the effects of drought by increasing the variation among individuals in CORT levels. Further examination of population level CORT responses to largescale environmental perturbations across a range of localized environmental conditions may be necessary to truly separate out such individual effects.

MANAGEMENT IMPLICATIONS

The possibility of increasing drought frequency with projected climate change may represent an emerging management issue if the reduction in body condition we noted has associate population implications. Although it is possible for managers to address body condition directly by providing food and water resources in time of acute stress, the benefits of such programs for pheasants are largely unknown and likely highly localized (e.g., Krausman et al. 2006). Alternatively, managers may choose to lessen the impacts of drought by mitigating other environmental conditions with proven benefits to pheasant population dynamics. For example, during a drought, limited growth of winter wheat and pasture grasses can concentrate pheasants in areas with residual cover (e.g., CRP). Increasing the availability of CRP may help dampen the effects of drought by improving survival and reproduction, but emergency haying and grazing of CRP fields is common during drought. As CRP rules limit emergency management to certain enrollment practices, pheasant managers in areas facing increased drought frequency may wish to promote practices with more restrictive rules. Alternatively, policy makers may wish to consider altering CRP rules to account for the importance of maintaining residual cover during drought. Even if managers maintain more residual cover on the landscape, projected increases in drought frequency are likely to change pheasant population dynamics in the arid plains, with important implications for pheasant hunters and wildlife agencies.

ACKNOWLEDGMENTS

We thank S. Duncan, A. Bailey, C. Frock and two anonymous reviewers for comments on previous iterations of this manuscript, as well as the landowners who allowed us access to their lands and the volunteers, technicians and Nebraska Game and Parks Commission employees who helped with data collection. The Nebraska Cooperative Fish and Wildlife Research Unit is supported by a cooperative agreement among the U.S. Geological Survey, the Nebraska

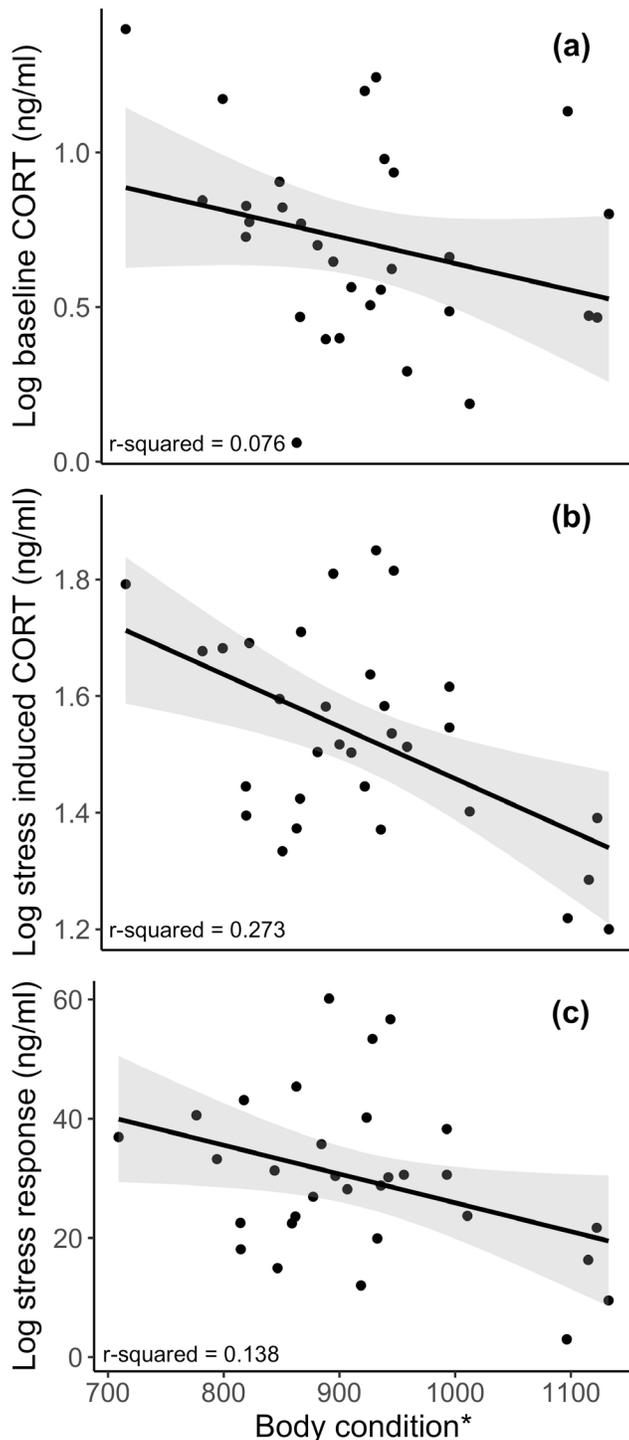


Figure 2. Baseline CORT (a), stress-induced CORT (b) and stress induced - baseline CORT (c) were negatively correlated with body condition in female ring-necked pheasants in southwestern Nebraska, USA, 2011–2012. Females in better condition had lower baseline CORT, stress-induced CORT and a smaller stress response. Data include all birds for which we assess CORT measures. Solid lines represent trend lines and dotted lines represent 95% CI. *Body condition was calculated by correcting mass for capture date using the formula: $M_d = M_i [C_o/C_i]^b$ OLS where M_i and C_i are the mass and capture date of the individual, C_o is the population mean capture date and b , the slope of the regression of $\ln(\text{mass})$ by $\ln(\text{capture Julian date})$ for all individuals in the population. The calculation was repeated in order to correct the newly calculated mass by tarsus length ($M_c = M_d [T_o/T_i]^b$ SMA; Peig and Green 2009).

Game and Parks Commission, the University of Nebraska-Lincoln, the U.S. Fish and Wildlife Service, and the Wildlife Management Institute. Funding was provided by Federal Aid in Wildlife Restoration Project W-98-R, administered by the Nebraska Game and Parks Commission. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

LITERATURE CITED

- Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, C. H. Flather, P. D. Culbert, B. D. Wardlow, and V. C. Radeloff. 2009. Effects of drought on avian community structure. *Global Change Biology* 16:2158–2170.
- Alley, R. B., J. Marotzke, W. D. Nordhaus, J. T. Overpeck, D. M. Peteet, R. A. Pielke, R. T. Pierrehumbert, P. B. Rhines, T. F. Stocker, L. D. Talley, and J. M. Wallace. 2003. Abrupt Climate Change *Science* 299:2005–2010.
- Bartholomew, G. A., and T. J. Cade. 1963. The water economy of land birds. *Auk* 80:504–539.
- Baskett, T. S. 1947. Nesting and production of the ring-necked pheasant in north-central Iowa. *Ecological Monographs* 17:1–30.
- Bates, D., M. Martin, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using {lme4}. *Journal of Statistical Software* 67:1–48.
- Blair, J. M., T. C. Todd, and M. A. Callahan. 2000. Responses of grassland soil invertebrates to natural and anthropogenic disturbances. Pages 43–71 in D. C. Coleman and P. F. Hendrix, editors. *Invertebrates as Webmasters in Ecosystems*. The Centre for Agricultural and Bioscience International, Wallingford, UK.
- Breitenbach, R. P., C. L. Nagra, and R. K. Meyer. 1963. Effect of limited food intake on cyclic annual changes in ring-necked pheasant hens. *Wildlife Monographs* 27:24–36.
- Brown, D. R., and T. W. Sherry. 2006. Food supply controls the body condition of a migrant bird wintering in the tropics. *Oecologia* 149:22–32.
- Chesness, R. A., M. M. Nelson, and W. H. Longley. 1968. The effect of predator removal on pheasant reproductive success. *Journal of Wildlife Management* 32:683–697.
- Christman, B. J. 2002. Extreme between-year variation in productivity of a bridled titmouse (*Baeolophus wollweberi*) population. *Auk* 119:1149.

- Clark, G. A. J. 1979. Body weights of birds: A review. *Condor* 81:193–202.
- Clark, W. R., T. R. Bogenschutz, and D. H. Tessin. 2008. Sensitivity analyses of a population projection model of ring-necked pheasants. *Journal of Wildlife Management* 72:1605–1613.
- Dahlgren, R. B. 1998. Distribution and abundance of the ring-necked pheasant in North America. Pages 29–43 in D. L. Hallet, W. R. Edwards, and B. G. V, editors. *Pheasants: Symptoms of Wildlife Problems on Agricultural Lands*. The Wildlife Society, Bloomington, Indiana, USA.
- Dahlgren, D. 2013. Pheasant Crowing Survey - 2013. Performance Report Statewide Wildlife Research and Surveys 1–10. Kansas Department of Wildlife, Parks, and Tourism, Pratt, Kansas, USA.
- Decker, K. L., C. J. Conway, and J. J. Fontaine. 2012. Nest predation, food, and female age explain seasonal declines in clutch size. *Evolutionary Ecology* 26:683–699.
- Draycott, R. A. H., A. N. Hoodless, M. N. Ludiman, and P. A. Robertson. 1998. Effects of spring feeding on body condition of captive-reared ring-necked pheasants in Great Britain. *Journal of Wildlife Management* 62:557–563.
- Dumke, R. T., and C. M. Pils. 1979. Renesting and dynamics of nest site selection by Wisconsin pheasants. *Journal of Wildlife Management* 43:705–716.
- Fried, L. A. 1940. The food habits of the ring-necked pheasant in Minnesota. *Journal of Wildlife Management* 4:27–36.
- Garnier, J., and M. A. Lewis. 2016. Expansion under climate change: The genetic consequences. *Bulletin of Mathematical Biology* 78:2165–2185.
- Gates, J. M. 1966. Renesting behavior in the ring-necked pheasant. *Wilson Bulletin* 78:309–315.
- Gates, J. M., E. J. Frank, and E. E. Woehler. 1970. Management of pheasant nesting cover on upland sites in relation to cropland diversion programs. Wisconsin Department of Natural Resources, Research Report 48:22, Madison, Wisconsin, USA.
- Hill, D. A. 1985. The feeding ecology and survival of pheasant chicks on arable farmland. *Journal of Applied Ecology* 22:645–654.
- Hoerling, M., J. Eischeid, A. Kumar, R. Leung, A. Mariotti, K. Mo, S. Schubert, and R. Seager. 2014. Causes and predictability of the 2012 Great Plains drought. *Bulletin of the American Meteorological Society* 95:269–282.
- Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5:365–374.
- Ji, L., and A. J. Peters. 2003. Assessing vegetation response to drought in the northern Great Plains using vegetation and drought indices. *Remote Sensing of Environment* 87:85–98.
- Johnson, S. N., J. T. Staley, F. A. L. McLeod, and S. E. Hartley. 2011. Plant-mediated effects of soil invertebrates and summer drought on above-ground multitrophic interactions. *Journal of Ecology* 99:57–65.
- Jordano, P. 1988. Diet, fruit choice and variation in body condition of frugivorous warblers in Mediterranean scrubland. *Ardea* 76:193–209.
- Jump, A. S., and J. Penuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters* 8:1010–1020.
- Kitaysky, A. S., J. C. Wingfield, and J. F. Piatt. 1999. Dynamics of food availability, body condition and physiological stress response in breeding Black-legged Kittiwakes. *Functional Ecology* 13:577–584.
- Knapp, A. K., C. J. W. Carroll, E. M. Denton, K. J. La Pierre, S. L. Collins, and M. D. Smith. 2015. Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia* 177:949–957.
- Krausman, P. R., S. S. Rosenstock, and J. W. Cain III. 2006. *Developed Waters for Wildlife: Science, Perception, Values, and Controversy*. Wildlife Society Bulletin 34:563–569.
- Labisky, R. F. 1968. Nightlighting: Its use in capturing pheasants, prairie chickens, bobwhites, and cottontails. *Illinois Natural History Survey Biological Notes* 62:1–12.
- Leif, A. P. 1994. Survival and reproduction of wild and pen-reared ring-necked pheasant hens. *Journal of Wildlife Management* 58:501.
- Mallya, G., L. Zhao, X. C. Song, D. Niyogi, and R. S. Govindaraju. 2013. 2012 Midwest drought in the United States. *Journal of Hydrologic Engineering* 18:737–745.
- Martin, T. E. 1987. Food as a limit on breeding birds: A life-history perspective. *Annual Review of Ecology and Systematics* 18:453–487.
- Mooij, W. M., R. E. Bennetts, W. M. Kitchens, and D. L. DeAngelis. 2002. Exploring the effect of drought extent and interval on the Florida snail kite: interplay between spatial and temporal scales. *Ecological Modelling* 149:25–39.
- National Agricultural Statistics Service [NASS]. 2017. Quick Stats page. <<https://quickstats.nass.usda.gov>>. Accessed March 2017.
- National Oceanic and Atmospheric Administration [NOAA]. 2016. National Centers for Environmental Information [NCEI]. Land-Based Station Data: Trenton Dam, NE, Culbertson, NE, McCook NE. <www.ncdc.noaa.gov/data-access/land-based-station-data>. Accessed May 2016.
- National Oceanic and Atmospheric Administration [NOAA]. 2017. National Centers for Environmental Information [NCEI]. Data Tools. <www.ncdc.noaa.gov/cdo-web/datatools/normal>. Accessed March 2017.

- Patterson, M. P., and L. B. Best. 1996. Bird abundance and nesting success in Iowa CRP fields: The importance of vegetation structure and composition. *American Midland Naturalist* 135:153–167.
- Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891.
- Petersen, L. R., R. T. Dumke, and J. M. Gates. 1988. Pheasant survival and the role of predation. Pages 165–196 in D. L. Hallett, W. R. Edwards, and G. V. Burger, editors. *Pheasants: Symptoms of Wildlife Problems on Agricultural Lands*. North Central Section of the Wildlife Society, Bloomington, Indiana, USA.
- Rich, E. L., and L. M. Romero. 2005. Exposure to chronic stress downregulates corticosterone responses to acute stressors. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology* 288:R1628–R1636.
- Rippey, B. R. 2015. The U.S. drought of 2012. *Weather and Climate Extremes* 10:57–64.
- Robb, L. A., K. Martin, and S. J. Hannon. 1992. Spring body condition, fecundity and survival in female willow ptarmigan. *Journal of Animal Ecology* 61:215–223.
- Rogers, R. D. 2002. Effects of wheat-stubble height and weed control on winter pheasant abundance. *Wildlife Society Bulletin* 30:1099–1112.
- Romero, L. M., and M. Wikelski. 2001. Corticosterone levels predict survival probabilities of Galapagos marine iguanas during El Niño events. *Proceedings of the National Academy of Sciences* 98:7366–7370.
- Romero, M. L. 2002. Seasonal changes in plasma glucocorticoid concentrations in free-living vertebrates. *General and Comparative Endocrinology* 128:1–24.
- Romero, M. L. 2004. Physiological stress in ecology: lessons from biomedical research. *Trends in Ecology and Evolution* 19:249–255.
- Sapolsky, R. M., L. M. Romero, and A. U. Munck. 2000. How do glucocorticoids influence stress responses? Integrating permissive, suppressive, stimulatory, and preparative actions. *Endocrine reviews* 21:55–89.
- Schoech, S. J., M. L. Romero, I. T. Moore, and F. Bonier. 2013. Constraints, concerns and considerations about the necessity of estimating free glucocorticoid concentrations for field endocrine studies. *Functional Ecology* 27:1100–1106.
- Shafer, M., D. Ojima, J. M. Antle, D. Kluck, R. A. McPherson, S. Peterson, B. Scanlon, and K. Sherman. 2014. Great Plains. Pages 441–461 in J. M. Melillo, T. C. Richmond, and G. W. Yohe, editors. *Climate Change Impacts in the United States: The Third National Climate Assessment*. U.S. Global Change Research Program, Washington, D.C., USA.
- Siegel, H. S. 1980. Physiological stress in birds. *BioScience* 30:529–534.
- Simonsen, V. L., and J. J. Fontaine. 2016. Landscape context influences nest survival in a Midwest grassland. *Journal of Wildlife Management* 80:877–883.
- Smith, S. A., N. J. Stewart, and E. J. Gates. 1999. Home ranges, habitat selection and mortality of ring-necked pheasants (*Phasianus colchicus*) in north-central Maryland. *American Midland Naturalist* 141:185–197.
- Snyder, W. D. 1985. Survival of radio-marked hen ring-necked pheasants in Colorado. *Journal of Wildlife Management* 49:1044–1050.
- Suchy, W. J., M. R. J., and J. M. Kienzler. 1991. Results of the August roadside survey for upland wildlife in Iowa: 1963–1988. *Journal of the Iowa Academy of Sciences* 98:82–90.
- Thomas, C. D., A. Cameron, R. E. Green, M. Bakkenes, L. J. Beaumont, Y. C. Collingham, B. F. N. Erasmus, M. F. de Siqueira, A. Grainger, L. Hannah, L. Hughes, B. Huntley, A. S. van Jaarsveld, G. F. Midgley, L. Miles, M. A. Ortega-Huerta, A. Townsend Peterson, O. L. Phillips, and S. E. Williams. 2004. Extinction risk from climate change. *Nature* 427:145–148.
- Tilman, D., and A. El Haddi. 1992. Drought and biodiversity in grasslands. *Oecologia* 89:257–264.
- Tompkins, D. M., G. Dickson, and P. J. Hudson. 1999. Parasite-mediated competition between pheasant and grey partridge: a preliminary investigation. *Oecologia* 119:378–382.
- Wada, H., T. P. Hahn, and C. W. Breuner. 2007. Development of stress reactivity in white-crowned sparrow nestlings: Total corticosterone response increases with age, while free corticosterone response remains low. *General and Comparative Endocrinology* 150:405–413.
- Walsh, J., D. Wuebbles, K. Hayhoe, J. Kossin, K. Kunkel, G. Stephens, P. Thorne, R. Vose, M. Wehner, J. Willis, D. Anderson, S. Doney, R. Feely, P. Hennon, V. Kharin, T. Knutson, F. Landerer, T. Lenton, J. Kennedy, and R. Somerville. 2014. Our changing climate. Pages 19–67 in J. M. Melillo, T. C. Richmond, and G. W. Yohe, editors. *Climate Change Impacts in the United States: The Third National Climate Assessment*. U.S. Global Change Research Program, Washington, D.C., USA.
- Williams, C. T., A. S. Kitaysky, A. B. Kettle, and C. L. Buck. 2008. Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *General and Comparative Endocrinology* 158:29–35.
- Wilson, R. J., R. D. Drobney, and D. L. Hallett. 1992. Survival, dispersal, and site fidelity of wild female ring-necked pheasants following translocation. *Journal of Wildlife Management* 56:79–85.

- Wingfield, J. C. 2013. Ecological processes and the ecology of stress: the impacts of abiotic environmental factors. *Functional Ecology* 27:37–44.
- Wingfield, J. C., D. L. Maney, C. W. Breuner, J. D. Jacobs, S. Lynn, M. Ramenofsky, and R. D. Richardson. 1998. Ecological bases of hormone—behavior interactions: The “emergency life history stage.” *American Zoologist* 38:191–206.
- Wingfield, J. C., and R. M. Sapolsky. 2003. Reproduction and resistance to stress: When and how. *Journal of Neuroendocrinology* 15:711–724.

*Submitted 19 January 2017. Accepted 4 August 2017.
Associate Editor was Mark Vrtiska.*