

A peer-reviewed version of this preprint was published in PeerJ on 3 March 2015.

[View the peer-reviewed version](https://peerj.com/articles/814) (peerj.com/articles/814), which is the preferred citable publication unless you specifically need to cite this preprint.

Ross JD, Kelly JF, Bridge ES, Engel MH, Reinking DL, Boyle WA. 2015. Pallid bands in feathers and associated stable isotope signatures reveal effects of severe weather stressors on fledgling sparrows. PeerJ 3:e814 <https://doi.org/10.7717/peerj.814>

1 **Fault bars and stable isotope signatures reveal effects of severe**
2 **weather stressors on fledgling sparrows**

3 **SHORT TITLE:** Stable isotopes in fault bars
4

5 **CORRESPONDING AUTHOR:**

6 **JEREMY D. ROSS**, Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK
7 73019, USA

8 Email: rossjd@ou.edu

9 Phone: 405-325-7053

10 **CO-AUTHORS:**

11 **JEFFREY F. KELLY**, Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK
12 73019, USA; Department of Biology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, USA

13 **ELI S. BRIDGE**, Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK

14 **MICHAEL H. ENGEL**, ConocoPhillips School of Geology and Geophysics, University of Oklahoma, 100 East Boyd
15 Street, Norman, Oklahoma 73019, USA

16 **DAN L. REINKING**, Sutton Avian Research Center, Oklahoma Biological Survey, University of Oklahoma, P.O. Box
17 2007, Bartlesville, OK 74005, USA

18 **W. ALICE BOYLE**, Division of Biology, 307 Ackert Hall, Kansas State University, Manhattan, Kansas 66506, USA

19 **Abstract**

20 In August 2013, we observed a high incidence (44%) of synchronous fault bars across the rectrices of
21 juvenile Grasshopper Sparrows (*Ammodrammus savannarum*) captured near El Reno, Oklahoma. Earlier
22 that year, on May 31, the site was struck by a severe storm which rained hailstones exceeding 5.5cm
23 diameter and spawned an historic 4.2km-wide tornado <8km to the south of the site. An assessment of
24 Grasshopper Sparrow nesting phenology indicated that a large number of nestlings were likely growing
25 tail feathers when the storm hit. To assess the nature of the fault bars, we measured $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$
26 stable isotope ratios within four 0.25-0.40mg feather sections taken from the distal end of a tail feather
27 from 18 juveniles captured at the site in August. The fault bar, if present, was contained within only one
28 section. Fault bars were located at various positions on the distal half of feathers, and fault bar width
29 significantly increased as a function of distance from the tip (i.e., age at formation). After correcting for
30 consistent, natural $\delta^{15}\text{N}$ variation across sections, we found that feather sections containing or located
31 immediately proximal to fault bars showed significantly higher $\delta^{15}\text{N}$ than sections from the same
32 feathers located distal to or further from the fault bar region. We also observed significantly higher $\delta^{13}\text{C}$
33 but lower $\delta^{15}\text{N}$ in the feathers of juveniles with fault bars compared to normal appearing juveniles. Our
34 findings support the hypothesis that an abrupt environmental stressor affected Grasshopper Sparrow
35 chicks of various ages, and caused short term catabolism of muscle tissue that resulted in a spike in $\delta^{15}\text{N}$
36 deposited into growing feathers. Furthermore, higher $\delta^{15}\text{N}$ and lower $\delta^{13}\text{C}$ among juveniles lacking fault
37 bars suggested a seasonal change in diet consistent with these individuals hatching after the May 31
38 storm. Severe weather events may represent major stressors to ground-nesting birds, and we
39 recommend exploiting opportunities to study the effects of severe weather as part of ongoing research
40 efforts.

41

42

43 **Keywords:** disturbance ecology, ground-nesting, hail, stress response, severe storm

44 Introduction

45 Growing feathers can log an inert record of environmental stressors being experienced by a bird.
46 For instance, stress during the time of feather tissue formation might be detectable as shifts in stable
47 isotope ratios (Hobson et al., 1993; Bortolotti et al., 2008; Bortolotti et al., 2009; Hatch, 2012; though see
48 Polito et al., 2011, Fairhurst et al., 2013) or visually-apparent structural and pigmentation deficiencies
49 known as fault bars (Riddle, 1908; Michner & Michner, 1938; Wood, 1950; Erritzøe & Busching, 2006;
50 Møller et al., 2009), Fault bars may result from severe fasting (Slagsvold, 1982), habitat degradation
51 (Sodhi, 2002), physical impairments (Møller, 1989), handling by human observers (King & Murphy, 1984;
52 Murphy et al., 1989; Negro et al., 1994), or disease (Romano et al., 2011). Such feather malformations
53 often coincide with endogenous spikes of stress hormones in the blood, particularly corticosterone
54 (DesRochers et al., 2009; Lattin et al., 2011; Legagneux et al., 2013), and are thought to form because
55 the deposition of keratin and melanin into the growing feather is disrupted (Michner & Michner, 1938;
56 Wood, 1950; Prum & Williamson, 2001; Møller et al., 2009). Consequently, fault bars can be readily
57 distinguished and studied for integrated signatures of past stressors experienced by wild bird
58 populations.

59 Fault bars are generally uncommon in natural bird populations. Among 86 European bird species
60 examined by Møller et al. (2009), the mean incidence of fault bars was only 5.6% and the maximum rate
61 of occurrence for any given species was 38.5%. Moreover, among individuals having fault bars, the
62 incidence of fault bars is rarely uniform across all feathers (Bortolotti et al., 2002; Møller et al., 2009),
63 which means the threshold for stress to induce fault bars likely varies among tracts of feathers (Jovani &
64 Blas, 2004; Serrano & Jovani, 2005). In August 2013 we observed an unusually high incidence of fault
65 bars among juvenile Grasshopper Sparrows (*Ammodrammus savannarum*) captured near El Reno,
66 Oklahoma; nearly half had prominent, pale-colored fault bars across their distal half of their rectrices.
67 All tail feathers were retained juvenile feathers with no freshly-molted tails were observed among the
68 juveniles captured. Since the distal half of juvenile tail feathers in this species grows from mid-way
69 through nestling development and continues through the early post-fledging period (Sutton, 1936;
70 Vickery, 1996; WAB, unpublished data) and young remain close to their natal site during the post-
71 fledging period (Smith, 1963; Hovick et al., 2011), these fault bars suggested that the local population
72 had been exposed to a widespread environmental stressor in the nest or shortly thereafter. The recent
73 meteorological history of the site led us to propose that the high incidence of fault bars resulted from a
74 severe hailstorm that struck the site on May 31, 2013 (Uccellini, 2014). We reasoned that the direct and

75 indirect effects of the hailstorm (i.e., impact trauma, abrupt ground-level cooling, and/or reduction in
76 insect prey resources) could have been sufficient to induce widespread stress within this population.

77 Stress responses in animals often involve muscle catabolism (Buchanan, 2000; Wingfield, 2008),
78 which equates to consumption of nitrogen at a trophic level higher than dietary sources (Waterlow,
79 1968; Hobson et al., 1993; Cherel et al., 2005; West et al., 2006). As a result of the transamination of
80 proteins during catabolism the ratio of heavy nitrogen isotopes (expressed as $\delta^{15}\text{N}$) is expected to
81 increase at higher trophic levels (Doucett et al., 1999), especially in the bloodstream and tissues with
82 high turnover rates such as the liver (Minagawa & Wada, 1984; Kelly, 2000; Post, 2002; Jardine et al.,
83 2005). Indeed during starvation stress events captive Japanese Quail (*Coturnix japonica*) chicks and
84 fasting wild female Ross' Geese (*Chen rossii*) showed significantly elevated $\delta^{15}\text{N}$ in muscle and liver
85 tissues relative to control groups (Hobson et al., 1993). Similar patterns were reported for fasting
86 penguins (Cherel et al., 2005; though see Polito et al., 2011), seals (Hückstädt et al., 2012), reptiles
87 (McCue & Pollock, 2008), spiders (Oelbermann & Scheu, 2002) and humans (Fuller et al., 2005). In
88 contrast, a restricted but not starvation diet was shown to actually reduce $\delta^{15}\text{N}$ among nestling seabirds
89 (Williams et al., 2007; Sears et al., 2009) and sparrows (Kempster et al., 2007), and fasting did not induce
90 $\delta^{15}\text{N}$ enrichment in whales (Aguilar et al., 2014). Stress-induced elevation of $\delta^{15}\text{N}$ is not necessarily
91 limited to starvation events as, for example, exposure to toxins without an effect on dietary intake can
92 have similar effects (Shaw-Allen et al., 2005; Sanpera et al., 2008).

93 Stable isotopes circulating in the blood are incorporated into growing feathers and these
94 signatures of conditions at the time of growth will be retained as part of the feather until the next molt
95 (Hobson, 1999; Kelly, 2000; West et al., 2006). Since both elevated $\delta^{15}\text{N}$ and the formation of fault bars
96 could be expected to coincide during stress events, we predicted that feather tissues comprising fault
97 bars would contain spikes in $\delta^{15}\text{N}$. More broadly, we hypothesized that stable isotope patterns along
98 the length of a feather can serve as temporally-discrete archives of transient physiological responses to
99 environmental stressors. From single tail feathers sampled from juvenile Grasshopper Sparrows at our
100 study site we assessed stable isotope patterns at two levels: 1) across sections of individual feathers that
101 contained fault bars and 2) between juveniles showing fault bars versus juveniles without fault bars.
102 With the first comparison, we tested whether the fault bars were associated with a period of elevated
103 heavy nitrogen consistent with muscle catabolism as part of a stress response. With the second
104 comparison, we determined if there was evidence for trophic successional shifts in isotope ratios
105 indicative of a temporal separation between the groups. Finally, we also examined past records of
106 Grasshopper Sparrow nesting phenology in Oklahoma to determine whether it was likely that such a

107 large proportion of the juvenile cohort at our site could have experienced the May 31 hailstorm. This
108 study represents the first quantitative analysis of shifts in stable isotopes associated with fault bar
109 formation, demonstrates a novel use of feathers as indicators of past stress, and provides new insights
110 into the potential sublethal impacts of severe weather on developing birds.

111

112 **Methods**

113 Sample collection and feather measurements

114 During August 27-28, 2013 we captured juvenile Grasshopper Sparrows (*Ammodrammus*
115 *savannarum*) by mist-net within a 29.3ha grassland unit at the United State Department of Agriculture
116 Grazinglands Research Laboratory (GRL; N35.555, W98.041) near El Reno, Oklahoma. Banding and
117 feather sampling was conducted with permission to WAB from the U.S. Fish and Wildlife Service (permit
118 #23836) and from the state of Oklahoma's Wildlife Conservation Department (permit 5762). Our use of
119 animals followed protocols approved by University of Oklahoma Institutional Animal Care and Use
120 Committee (Animal Use Statement R12-019) and by the Kansas State University's Institutional Animal
121 Care and Use Committee (protocol 3260). As part of a standard sequence of morphological
122 measurements, we scored each juvenile's tail as having fault bars (i.e., evidence of reduced
123 pigmentation and/or structural weaknesses; Figure 2A) or having apparently normal feathers. We
124 photographed the entire tail, removed a single outer rectrix, and stored the feather in a labeled coin
125 envelope.

126 In the laboratory we photographed each sampled feather adjacent to a 0.5mm-scaled ruler,
127 under fixed light sources, and against separate white grid paper and matte black backgrounds. From the
128 pictures we measured length of the feathered rachis, width of the fault bar, and distance from the fault
129 bar midpoint to the feather tip using the program imageJ (Rasband, 2014). We evaluated the pairwise
130 correlation between these measures using Pearson's product-moment tests. We compared the total
131 vane length between fault bar and normal feathers using a t-test.

132 Observed pigmentation deficiencies in true fault bars should coincide with malformed feather
133 barbules (Michner & Michner, 1938; Wood, 1950; Prum & Williamson, 2001; Møller et al., 2009).
134 Therefore, we examined and photographed select feathers under a dissecting microscope equipped
135 with a digital camera. We noted the physical attributes of barbules within and adjacent to fault bars, as
136 well as in normal juvenile rectrices originally grown as nestlings or freshly replaced during the late-
137 summer post-juvenile molt.

138 Stable isotope analysis

139 In preparation for analysis we first cleaned each feather with dilute detergent and then a 2:1
140 chloroform–methanol solution (Paritte & Kelly, 2009) followed by oven-drying at 100°C. We then
141 sectioned the distal end of each feather into four or five 0.25-0.40 mg portions. The fault bar, if present,
142 was contained within only one of these sections (Figure 2B) and relative to this section we analyzed at
143 least two sections grown after (i.e., proximal) and all sections that preceded it (if possible). We packed
144 each section into a 3.5x5mm tin capsule for insertion into an autosampling tray. Measurements of
145 isotope ratios for nitrogen ($\delta^{15}\text{N}$) and carbon ($\delta^{13}\text{C}$) were performed at the University of Oklahoma with
146 a Thermo Delta V Plus isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany)
147 connected to a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies, Valencia, CA).

148 We applied two analytical approaches to the isotope data. First, we compared feathers from
149 juveniles showing fault bars versus those from normal juveniles using separate ANOVAs of the $\delta^{15}\text{N}$ and
150 $\delta^{13}\text{C}$ data, including the following explanatory variables: whole feather category (fault bar versus
151 normal), feather section (ordinal from tip), individual, and pairwise interactions of section*fault bar and
152 section*individual. In our second approach to analyzing the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data across sequential
153 sections (i.e., proximally from tip) we initially conducted separate linear regressions for each individual,
154 pooled the residuals, and fit these using a non-linear, second-order polynomial function. From the
155 residuals of this two-step fit we selected data from fault bar feathers only and conducted separate
156 ANOVAs for N and C using section position relative to the fault bar as the lone factor [i.e., containing,
157 immediately proximal, or outside (distal or >1 section proximal)]. This alternative approach improved
158 our ability to control for individual variation and natural patterns in stable isotopes by age (i.e., across
159 sections) within the population, enabling us to identify relative spikes in stable isotope ratios among
160 feather sections relative to fault bars.

161 *Weather and Grasshopper Sparrow breeding phenology*

162 We reviewed the recent management history of the grassland unit through communication with
163 GRL staff to determine if any anthropogenic disturbance may have occurred at that site during the 2013
164 breeding season. Additionally, we examined local-scale meteorology during 2013 relative to 1999-2012
165 means using data from the 'ELRE' Oklahoma Mesonet station at the GRL
166 (http://www.mesonet.org/index.php/sites/site_description/elre). The only notable anomaly was a
167 severe thunderstorm that occurred on May 31, 2013. We consulted National Weather Service reports on
168 this storm, including: hail observer reports made through the Severe Hazards Analysis & Verification
169 Experiment (*SHAVE*; Ortega et al., 2009) and hail estimates derived from weather RADAR data using the
170 Maximum Estimated Size of Hail (MESH) model (Witt et al., 1998; Stumpf et al., 2004).

171 We evaluated whether the May 31 storm could have affected such a large proportion of juvenile
172 birds at our study site by examining the species' nesting phenology in Oklahoma. One of the authors
173 (DLR) had previously collected such data for 149 Grasshopper Sparrow nests 200km to the northeast in
174 Washington and Osage Counties, Oklahoma from 1992 to 1996 as part of a separate study by the
175 George M. Sutton Avian Research Center [GMSARC; see Rohrbaugh et al. (1999) for the nest searching
176 methodology]. Using the 1992-1996 nest phenology data we calculated what proportion of an average
177 Oklahoma Grasshopper Sparrow cohort would have hatched by May 31 and then used a z-test to
178 determine whether this was statistically different than the proportion of juveniles showing fault bars
179 among those captured in late August 2013. We performed all statistical analyses in R (R Core Team,
180 2014).

181 182 **Results**

183 Fault bar incidence and feather characteristics

184 Grasshopper Sparrow juveniles captured from the GRL population displayed a very high
185 incidence of synchronous fault bars in the tail (11 of 25 individuals; 44%). This far exceeded the 1.5%
186 rate at which similar fault bars occurred among 271 juveniles captured in 2013-14 at 22 sites in
187 Nebraska, Kansas, and Oklahoma by one of the authors (WAB, unpublished data). Compared to species-
188 specific rates reported by Møller et al. (2009) the incidence of fault bars among Grasshopper Sparrows
189 at the GRL in 2013 did not differ from *Corvus corone* (38.5%, n=13, z=0.326, p=0.741) or *Streptopelia*
190 *decaocto* (25%, n=8, z=0.957, p=0.169), although it significantly exceeded rates from any of the 84 other
191 species they examined. Among the 25 juveniles examined we noted fault bars on the wing feathers for
192 only one individual, and these were narrow and slightly asynchronous (see Supplemental Information
193 Figure S2).

194 The fault bars we observed among Grasshopper Sparrow juveniles were up to 3.4mm wide,
195 aligned across all of the tail feathers, and showed modestly-reduced pigmentation and barbule density
196 (Figure 2A and 3). We found no difference in mean (\pm s.d.) vane length between feathers with and
197 without fault bars [fault bar: 41.0 (\pm 1.1) mm; normal: 41.0 (\pm 1.6) mm; $t = 0.127$, $p = 0.900$]. Among
198 feathers having fault bars, the mean distance from fault bar midpoint to feather tip was 8.8 (\pm 5.0) mm
199 and the mean fault bar width was 1.8 (\pm 0.9) mm. The relative position of fault bars ranged from 5.7%
200 to 42.3% the length of the vane [mean (\pm s.d.) = 21.4% (\pm 12.3%)]. Wider fault bars were located at more
201 basal locations along the feather ($r = 0.928$; $t = 7.45$; $p < 0.001$) but were not related to vane length ($r =$
202 0.018 ; $t = 0.05$; $p = 0.958$). The locations of fault bars were likewise not correlated with vane length ($r =$

203 -0.025; $t = -0.075$; $p = 0.942$). We observed that the structure of feather barbules was notably
204 degraded in fault bars, evident as large sections of unhooked or entirely missing barbules (Figure 3).

205 Stable isotopes

206 Variation in $\delta^{15}\text{N}$ was explained by fault bar presence ($F = 327.2$, $df = 1$, $p < 0.001$), individual
207 differences ($F = 50.3$, $df = 16$, $p < 0.001$), feather section ($F = 8.8$, $df = 1$, $p = 0.005$) and feather section by
208 individual interactions ($F = 2.4$, $df = 1$, $p = 0.016$). Likewise, variation in $\delta^{13}\text{C}$ was associated with fault
209 bar presence ($F = 23.9$, $df = 1$, $p < 0.001$), individual differences ($F = 18.6$, $df = 16$, $p < 0.001$), feather
210 section ($F = 14.6$, $df = 1$, $p < 0.001$) and feather section by individual interactions ($F = 1.9$, $df = 1$, $p =$
211 0.050). Differences between normal and fault bar feathers were driven by the former having higher
212 $\delta^{15}\text{N}$ (mean difference = 2.2‰) but lower levels of $\delta^{13}\text{C}$ (mean difference = -1.2‰ ; see Supplemental
213 Information for complete results).

214 Our analysis of sections within fault bar feathers indicated that, after correcting for individual
215 and population variation, there were no significant difference among sections in terms of either $\delta^{15}\text{N}$ (F
216 $= 2.22$, $df = 2$, $p = 0.121$) or $\delta^{13}\text{C}$ ($F = 0.42$, $df = 2$, $p = 0.661$). However, if we pooled data from sections
217 containing fault bars with those subsequently grown in immediately proximal sections, then relative to
218 the sections outside the fault bar region these sections contained elevated $\delta^{15}\text{N}$ ($t = -2.11$, $p = 0.040$;
219 Figure 4) but similar ratios of $\delta^{13}\text{C}$ ($t = -0.92$, $p = 0.364$).

220 Stress events and breeding phenology

221 Based on both weather radar and ELRE Mesonet data we estimated that hail fell over the GRL
222 during approximately 16:00-16:20 local time on May 31, 2013. Hailstone diameters estimated from
223 weather radar data using the MESH model ranged from 4.45-5.72 cm at the GRL (Figure 1). Actual
224 hailstone sizes reported through SHAVE matched or exceeded the MESH estimates. For instance, 4.45
225 cm-diameter hailstones reported 26 km ESE of the GRL in Yukon, Oklahoma suitably matched the 3.81
226 cm estimates made using MESH, but reports of hailstone diameters of 3.18 cm and 4.45 cm at points 30
227 km WSW and 26 km WNW of the GRL, respectively, far exceeded the 1.91 cm maximum sizes estimated
228 by MESH for those locations.

229 Data from the 'ELRE' Oklahoma Mesonet station at the GRL indicated that during the period
230 when juveniles captured in August would have likely been in the nest (i.e., May 1st to July 13th, 2013) the
231 amount of precipitation recorded at the GRL was 67.0 cm. This exceeded this site's 1999-2012 mean by
232 22.4 cm and represented 150 % the normal rainfall for this period. Perhaps not surprisingly this
233 elevated total was primarily caused by a 12.1 cm downpour during the May 31 storm. No other daily
234 precipitation total exceeded 4.1 cm during this period. Local weather data did not suggest any other

235 possible stressors from weather. At no point between May 1st and July 13th, 2013 did the maximum or
236 minimum temperature depart more than $\pm 5^{\circ}\text{C}$ from 1999-2012 means. Other local stressors, such as
237 local land use and management, were similarly unlikely. During 2013 our grassland study site at the GRL
238 was grazed lightly by bulls (~1 per 10ha) and the area was not managed with herbicides, pesticides, or
239 mowing treatments during May-July (S. Coleman, USDA, pers. comm.)

240 The median date for clutch initiation observed in Oklahoma from 1992-96 as part of GMSARC
241 surveys was in late May (Table 1). These findings were consistent with anecdotal observations of the
242 species' breeding activity at the GRL in 2013-14 (JDR, unpublished data). Dates of clutch initiation,
243 either directly observed or extrapolated based on incubation stage at discovery, were compiled from the
244 GMSARC data according to their expected status on May 31 of that year. For Grasshopper Sparrows, a
245 typical clutch of 4 eggs will hatch approximately 14 days after the first egg is laid and the young fledge
246 after 10-12 days in the nest (Vickery, 1996). According to this schedule, by the afternoon of May 31,
247 clutches initiated prior to May 5 would have fledged, clutches initiated May 5-18 would be nestlings, and
248 clutches initiated May 19-31 would still be eggs (Table 1). Clutch initiation dates indicated that in a
249 typical year 27.6% of a Grasshopper Sparrow cohort would have hatched or fledged by May 31. This
250 proportion was marginally lower than the observed proportion (44%) of juveniles captured at the GRL in
251 August 2013 that had fault bars ($z=1.64$; $p=0.051$).

252 **Discussion**

253 Our findings are all consistent with fault bars among juvenile Grasshopper Sparrows at GRL likely
254 resulting from an intense regional-scale stressor: the May 31, 2013 severe storm that impacted the
255 region with tornadoes, damaging winds, and large hail (Uccellini, 2014). For a ground-nesting species
256 the immediate and short-term impacts of this rare event, particularly the hailstones exceeding 5cm
257 diameter, are a likely candidate to cause widespread physiological stress among dependent young.
258 Beyond this simple event attribution, our findings provide some of the first evidence about the sublethal
259 impacts of severe weather and how native bird species may be affected by such periodic stressors.

260 Stable isotopes as records of environmental stressors

261 Nitrogen isotopes within the fault bar region were significantly enriched with heavy nitrogen
262 relative to other parts of the same feathers. These spikes in $\delta^{15}\text{N}$ support our predictions and are
263 consistent with increased muscle catabolism as part of the stress response that produced the fault bars.
264 Notably, we found significant among-individual variation both in the slope and magnitude of nitrogen
265 and carbon fractionation across feather sections, which suggested differences in diets during
266

267 development in line with these young originating from different nests. This lends confidence to these
268 individuals representing a broad sampling of variation in the population.

269 The magnitude of differences between feathers from juveniles possessing normal feathers
270 versus juveniles displaying fault bars for both $\delta^{13}\text{C}$ (-1.2‰) and $\delta^{15}\text{N}$ (2.2‰) would be consistent with
271 trophic or successional (i.e., C4 to C3 plant community) shifts that one might expect among individuals
272 growing feathers at different times during a temperate breeding season (Kelly, 2000). More specifically,
273 if we assume that juveniles without fault bars were reared after the large scale disturbance, then the
274 data are consistent with a scenario in which Grasshopper Sparrow nestling and fledglings' diets changed
275 moderately through the season. Increased $\delta^{15}\text{N}$ in feathers without fault bars could be attributed to
276 ingestion of insect prey items at higher trophic levels, and the difference in $\delta^{13}\text{C}$ could result from an
277 increasingly C3 plant base (Hobson, 1999; Kelly, 2000; West et al., 2006). This trophic progression is
278 even evident within individual feathers, as $\delta^{15}\text{N}$ naturally increases from tip-to-root, as observed by
279 Symes and Woodborne (2011) in White-bellied Sunbirds (*Cinnyris talatala*).

280 Fault bars as a response to stress

281 High rates of fault bars have been reported in other species, (i.e., >90% in raptors; Hawfield,
282 1986; Bortolotti et al., 2002), but these accounts describe isolated, narrow (i.e., ≤ 1 mm) fault bars that
283 show an extreme degree of structural degradation. These accounts in the literature and our own
284 observations suggest that there are two types of fault bars that appear in bird feathers. We argue that
285 fault bars like the ones observed in our Grasshopper Sparrows result from stressful experiences that
286 lead to transient reductions in the quality of growing feathers. As for the narrower isolated type of fault
287 bars, we subscribe to Michener & Michener's (1938) original assertion that they arise due to haphazard
288 and short-lived disruptions to development such as a temporary reduction of circulation or minor injury
289 to the growing follicle. Experimental studies are needed to determine the basis for different fault bar
290 types.

291 There was a strong linear relationship between position of the fault along the length of the
292 feather and the width of the fault bar. If fault bars represent a malformed portion of a growth bar and
293 each growth bar represents a set period of growth (Grubb, 2006; Jovani & Diaz-Real, 2012), then this
294 pattern could indicate that feather growth linearly increased as the feather became longer. However,
295 Elderbrock et al. (2012) found that although width of growth bars down the vane of individual feathers
296 in juvenile Eastern Bluebirds (*Sialia sialis*) did vary substantially, these differences were randomly
297 located and did not linearly increase with position down the feather vane. Instead, the authors noted
298 that growth bar width was disconnected from the rate of feather elongation, which was constant during

299 the development of individual feathers. Therefore, rather than feather growth increasing with age the
300 increasing fault bar width could alternatively indicate that the duration of the stress response itself had
301 linearly increased as a function of chick age. This inference agrees with prior studies showing that older
302 chicks are more prone to an extended stress response, either due to increased development of the
303 hypothalamic-pituitary-adrenal axis (Sims & Holberton, 2000; Sockman & Schwabl, 2001; Wada et al.,
304 2007) or because they have greater dietary intake demands and are closer to starvation than younger
305 chicks (Blem, 1975).

306 Ecological and evolutionary implications of fault bars

307 Fault bars are likely to be associated with reduced fitness and, therefore, may be subject to
308 selective pressures. For example, Goshawk (*Accipiter gentilis*) prey had significantly higher-than-average
309 incidences of fault bars (Møller et al., 2009). In addition, fault bars are more prone to breakage (Sarasola
310 & Jovani, 2006), which affects flight performance (Murphy et al., 1989; Norberg, 1990; Jovani et al.,
311 2010), and fault bars can be subject to sexual selection as a signal of individual condition (Blanco & de la
312 Puente, 2002). Jovani & Blas (2004), however, argued that fault bars occur non-randomly among
313 feather tracts. Their “fault bar allocation hypothesis” predicts that selective pressures will favor
314 resource allocation toward feathers most critical to flight performance, namely the primary remiges of
315 the wing, at the expense of less essential feather growth (e.g., rectrices). Hence, the allocation
316 hypothesis would predict that fault bar formation in the tail, for instance, would reflect an adaptation
317 that allows birds experiencing nutritional stress to preferentially better develop feathers that are
318 fundamental to powered flight.

319 Fault bar allocation may be particularly important for juvenile birds which have intense resource
320 demands as their body and flight feathers grow synchronously (Dolnik & Gavrilov, 1979). Quickly
321 growing remiges to hasten sustained flight is likely paramount to juvenile survival. Juveniles do display
322 higher incidences of fault bars than adults (Hawfield, 1986; Jovani & Blas, 2004; Jovani & Diaz-Real,
323 2012), especially among feathers less critical to flight such as rectrices (King & Murphy, 1984; Bortolotti
324 et al., 2002; Serrano & Jovani, 2005; Sarasola & Jovani, 2006; Jovani et al., 2010). Yet, in many species
325 (including Grasshopper Sparrows) juvenile feathers containing fault bars must be retained only through
326 the relatively brief post-fledging period to be replaced with high-quality feathers during post-juvenile
327 molt, reducing possible carry-over effects during the stresses of migration and/or winter (Pap et al.,
328 2007). Among the Grasshopper Sparrows showing fault bars the mean age was likely less than 12 days
329 old at the time of the stressor [based on tail growth rates reported by Sutton (1936) and WAB,
330 unpublished data]. By this age the growth of remiges would have only been partially completed (Sutton,

331 1936), yet in only one case did we observe fault bars in the wing that were apparently concordant with
332 fault bars in the tail. It seems probable that ground nesting birds like Grasshopper Sparrows, which are
333 frequently exposed to environmental stressors (Nice, 1957; Ricklefs, 1969), would benefit by coupling
334 fault bar allocation with post-juvenile molt as an adaptive response to stress during early development.

335 Biological relevance of severe weather

336 Local environmental conditions dictate whether species survive and reproduce successfully in
337 any given area. Lack (1966) suggested that extremes in local environments would be strongly
338 responsible for limiting species, as these would present the most grievous of stressors. Severe weather
339 is a prime example, as it can cause widespread mortality and is known to necessitate specific local
340 adaptations within local biological communities (Wingfield, 1988; Newton, 2007). Severe weather
341 impacts on birds have generally been studied in association with large, widespread, and relatively long-
342 lasting events such as cold snaps, hurricanes, and blizzards (Whitmore et al., 1977; Wiley & Wunderle,
343 1993; Brown & Brown, 1998; Newton, 2007; Fredericksen et al., 2008; Rittenhouse et al., 2010). Yet,
344 intense but relatively localized perturbations such as severe hailstorms or tornadoes have received little
345 scientific attention, outside of anecdotal or case-study reports [see Ross (*in prep*) for a complete
346 review]. These events can vary in their degree of impact across species and thus may represent a
347 particularly strong factor in regulating species distributions. Considering that much of the American
348 Great Plains experiences severe thunderstorms and hail annually (Doswell et al., 2005; Cinteneo et al.,
349 2012) and that hailstones as small as 1cm diameter can destroy eggs and injure adults (Ross, *in prep*),
350 these weather events are likely to have profound ecological and conservation relevance to grassland
351 species, especially ground-nesting birds. This is especially true during the key breeding period of April-
352 July, when vulnerable adults, eggs, and young face the peak of the severe thunderstorm season.

353 In our study, if we assume that Grasshopper Sparrow juveniles with 'normal' rectrices had
354 hatched after May 31, our analysis indicated that such individuals were marginally less abundant than
355 expected based on the species' nesting phenology in Oklahoma (i.e., 56% in 2013 versus 72.4% in 1992-
356 96). This could be explained by local climatic differences, such as the date of last spring freeze. This is
357 currently only slightly earlier at GRL (Canadian County) than Osage County (Oklahoma Climatological
358 Survey, 2014), though 20-years of climate change between these periods could explain an earlier shift in
359 nesting phenology. Alternatively, the lower proportion of late-hatching young in 2013 could have
360 reflected an actual net loss among the latter half of the 2013 cohort, in this case ~23% relative to the
361 1992-96 demography. It is probable that hailstones exceeding 4cm-diameter could have led to

362 widespread destruction of eggs and that this stressor disrupted late-season nesting attempts (e.g.,
363 adults directly killed or abandoned the area after a storm; Ross, *in prep*).

364 During extremely heavy hailstorms nesting parents may flee, leaving young exposed to the
365 weather (Hanford, 1913; Hume, 1986; Kirkpatrick et al., 2009). Recently-fledged Grasshopper Sparrow
366 young are quite vulnerable to exposure (Hovick et al., 2011) and would, therefore, be expected to be
367 widely stressed during severe thunderstorms. Young that survive 'riding the storm out' may be
368 traumatized by the event itself or because of reduced provisioning by adults. If so, we may expect these
369 offspring to show lasting signs of developmental stress such as the degraded feather structure typical of
370 fault bars (DesRochers et al., 2009; Lattin et al., 2011; Legagneux et al., 2013).

371 Scientifically assessing the biological impacts of severe weather is commonly viewed as being
372 limited by our ability to predict well in advance where storms will strike so that we may organize before
373 and after comparisons. However, each year field studies are likely to occur at points throughout
374 regions where severe weather often occurs (Doswell et al., 2005; Cecil & Blankenship, 2012; Cinteneo et
375 al., 2012) and these researchers would be well-positioned to opportunistically study the ecological
376 consequences of severe weather. We call for the ecological research community, to take advantage of
377 severe storm events as they occur at their research sites, opportunistically sampling biologically
378 informative data required to assess the nature and magnitude of such stressors on animal communities.
379 In the face of a changing climate and the expected shifts in severe weather regimes (Trapp et al., 2007;
380 Goodess, 2013) there is a need to expand our knowledge of the both current and future ecological
381 impacts of severe weather events (Jentsch et al., 2007) so that we may work toward mitigating losses
382 among vulnerable species and biological communities.

383

384 **Acknowledgements**

385 We thank the U.S. Department of Agriculture's Grazinglands Research Laboratory, The Nature Conservancy's
386 Tallgrass Prairie Preserve, and individual landowners for allowing field access. S. Engel prepared the feather
387 tissues for stable isotope analysis. R. Maynard operated the stable isotope mass spectrometer-elemental analyzer
388 equipment. R. Rosenberg assisted capturing Grasshopper Sparrows in the field. This is contribution no. 15-168-J
389 from the Kansas Agricultural Experimental Station.

390 **References**

- 391 Aguilar A, Giménez J, Gómez-Campos E, Cardona L, Borrell A. 2014. $\delta^{15}\text{N}$ value does not reflect fasting in
392 mysticetes. PLoS ONE 9:e92288.
- 393 Blanco G, de la Puente J. 2002. Multiple elements of the Black-billed Magpie's tail correlate with variable honest
394 information on quality in different age/sex classes. Animal Behaviour 63:217–225.
- 395 Blem CR. 1975. Energetics of nestling House Sparrows *Passer domesticus*. Comparative Biochemistry and
396 Physiology Part A: Physiology 52:305–312.
- 397 Bortolotti GR, Dawson RD, Murza GL. 2002. Stress during feather development predicts fitness potential. Journal
398 of Animal Ecology 71:333–342.
- 399 Bortolotti GR, Marchant T, Blas J, Cabezas S. 2009. Tracking stress: localisation, deposition and stability of
400 corticosterone in feathers. The Journal of Experimental Biology 212:1477–82.
- 401 Bortolotti GR, Marchant T a., Blas J, German T. 2008. Corticosterone in feathers is a long-term, integrated measure
402 of avian stress physiology. Functional Ecology 22:494–500.
- 403 Brown CR, Brown MB. 1998. Intense natural selection on body size and wing and tail asymmetry in Cliff Swallows.
404 Evolution 52:1461–1475.
- 405 Buchanan KL. 2000. Stress and the evolution of condition-dependent signals. Trends in Ecology & Evolution
406 15:156–160.
- 407 Cecil DJ, Blankenship CB. 2012. Toward a global climatology of severe hailstorms as estimated by satellite passive
408 microwave imagers. Journal of Climate 25:687–703.
- 409 Cheral Y, Hobson K, Bailleul F, Groscolas R. 2005. Nutrition, physiology, and stable isotopes: new information
410 from fasting and molting penguins. Ecology 86:2881–2888.
- 411 Cintineo JL, Smith TM, Lakshmanan V, Brooks HE, Ortega KL. 2012. An objective high-resolution hail
412 climatology of the contiguous United States. Weather and Forecasting 27:1235–1248.
- 413 DesRochers DW, Reed JM, Awerman J, Kluge JA, Wilkinson J, van Griethuijsen LI, Aman J, Romero LM. 2009.
414 Exogenous and endogenous corticosterone alter feather quality. Comparative Biochemistry and Physiology Part
415 A: Molecular & Integrative Physiology 152:46–52.
- 416 Dolnik VR, Gavrilov VM. 1979. Bioenergetics of molt in the Chaffinch (*Fringilla coelebs*). The Auk 96:253–264.
- 417 Doswell C a., Brooks HE, Kay MP. 2005. Climatological estimates of daily local nontornadic severe thunderstorm
418 probability for the United States. Weather and Forecasting 20:577–595.
- 419 Doucett RR, Booth RK, Power G, McKinley RS. 1999. Effects of the spawning migration on the nutritional status of
420 anadromous Atlantic Salmon (*Salmo salar*): insights from stable-isotope analysis. Canadian Journal of Fisheries
421 and Aquatic Sciences 56:2172–2180.
- 422 Elderbrock EK, Kern MD, Lynn SE. 2012. Problems with using ptilochronology to measure the growth and
423 nutritional status of nestling bluebirds. The Condor 114:823–830.
- 424 Erritzøe J, Busching WD. 2006. Der aktuelle Forschungsstand und darauf folgende Überlegungen zu Hungerstreifen
425 und ähnlichen Phänomenen im Vogelgefieder. Beiträge zur Gefiederkunde und Morphologie der Vögel 12:52–
426 65.
- 427 Fairhurst GD, Vögeli M, Serrano D, Delgado A, Tella JL, Bortolotti GR. 2013. Can synchronizing feather-based
428 measures of corticosterone and stable isotopes help us better understand habitat-physiology relationships?
429 Oecologia 173:731–43.
- 430 Frederiksen M, Daunt F, Harris MP, Wanless S. 2008. The demographic impact of extreme events: stochastic
431 weather drives survival and population dynamics in a long-lived seabird. Journal of Animal Ecology 77:1020–
432 1029.
- 433 Fuller BT, Fuller JL, Sage NE, Harris D a, O'Connell TC, Hedges REM. 2005. Nitrogen balance and delta ^{15}N : why
434 you're not what you eat during nutritional stress. Rapid Communications in Mass Spectrometry 19:2497–506.
- 435 Goodess CM. 2013. How is the frequency, location and severity of extreme events likely to change up to 2060?
436 Environmental Science & Policy 27:S4–S14.
- 437 Grubb TC. 2006. Ptilochronology: Feather time and the biology of birds. New York, NY: Oxford University Press.

- 438 Hanford FS. 1913. Sierra storms and birds. *The Condor* 15:137–138.
- 439 Hatch KA. 2012. The use and application of stable isotope analysis to the study of starvation, fasting, and nutritional
440 stress in animals. In: McCue MD ed. *Comparative Physiology of Fasting, Starvation, and Food Limitation*.
441 Berlin, Heidelberg: Springer - Verlag, 337–364.
- 442 Hawfield EJ. 1986. The number of fault bars in the feathers of Red-tailed Hawks, Red-shouldered Hawks, Broad-
443 winged Hawks, and Barred Owls. *The Chat* 50:15–18.
- 444 Hobson KA. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–
445 326.
- 446 Hobson KA, Alisauskas RT, Clark RG. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and
447 nutritional stress: implications for isotopic analyses of diet. *The Condor* 95:388.
- 448 Hovick TJ, Miller JR, Koford RR, Engle DM, Debinski DM. 2011. Postfledging survival of Grasshopper Sparrows
449 in grasslands managed with fire and grazing. *The Condor* 113:429–437.
- 450 Hückstädt LA, Koch PL, McDonald BI, Goebel ME, Crocker DE, Costa DP. 2012. Stable isotope analyses reveal
451 individual variability in the trophic ecology of a top marine predator, the Southern Elephant Seal. *Oecologia*
452 169:395–406.
- 453 Hume RA. 1986. Reactions of birds to heavy rain. *British Birds* 79:326–329.
- 454 Jardine TD, Gray M a., McWilliam SM, Cunjak R a. 2005. Stable isotope variability in tissues of temperate stream
455 fishes. *Transactions of the American Fisheries Society* 134:1103–1110.
- 456 Jentsch A, Kreyling J, Beierkuhnlein C. 2007. A new generation of climate-change experiments: events, not trends.
457 *Frontiers in Ecology and the Environment* 5:365–374.
- 458 Jovani R, Blas J. 2004. Adaptive allocation of stress-induced deformities on bird feathers. *Journal of Evolutionary*
459 *Biology* 17:294–301.
- 460 Jovani R, Blas J, Stoffel MJ, Bortolotti LE, Bortolotti GR. 2010. Fault bars and the risk of feather damage in cranes.
461 *Journal of Zoology* 281:94–98.
- 462 Jovani R, Diaz-Real J. 2012. Fault bars timing and duration: the power of studying feather fault bars and growth
463 bands together. *Journal of Avian Biology* 43:97–101.
- 464 Kelly JF. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology.
465 *Canadian Journal of Zoology* 78:1–27.
- 466 Kempster B, Zanette L, Longstaffe FJ, MacDougall-Shackleton SA, Wingfield JC, Clinchy M. 2007. Do stable
467 isotopes reflect nutritional stress? Results from a laboratory experiment on song sparrows. *Oecologia* 151:365–
468 371.
- 469 King JR, Murphy ME. 1984. Fault bars in the feathers of White-crowned Sparrows: dietary deficiency or stress of
470 captivity and handling? *The Auk* 101:168–169.
- 471 Kirkpatrick C, Conway CJ, Ali MH. 2009. Sanitation of entire broods of dead nestlings may bias cause-specific nest
472 failure rates. *Ibis* 151:207–211.
- 473 Lack DL. 1966. *Population studies of birds*. Oxford: Clarendon Press.
- 474 Lattin CR, Reed JM, DesRochers DW, Romero LM. 2011. Elevated corticosterone in feathers correlates with
475 corticosterone-induced decreased feather quality: a validation study. *Journal of Avian Biology* 42:247–252.
- 476 Legagneux P, Harms NJ, Gauthier G, Chastel O, Gilchrist HG, Bortolotti G, Bêty J, Soos C. 2013. Does feather
477 corticosterone reflect individual quality or external stress in arctic-nesting migratory birds? *PLoS ONE*
478 8:e82644.
- 479 McCue MD, Pollock ED. 2008. Stable isotopes may provide evidence for starvation in reptiles. *Rapid*
480 *Communications in Mass Spectrometry* 22:2307–14.
- 481 Michener H, Michener JR. 1938. Bars in flight feathers with five sets of illustrations. *The Condor* 40:149–160.
- 482 Minagawa M, Wada E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation
483 between $\delta^{15}\text{N}$ and animal age. *Geochimica et Cosmochimica Acta* 48:1135–1140.
- 484 Møller AP. 1989. Viability costs of male tail ornaments in a swallow. *Nature* 339:132–135.
- 485 Møller AP, Erritzøe J, Nielsen JT. 2009. Frequency of fault bars in feathers of birds and susceptibility to predation.
486 *Biological Journal of the Linnean Society* 97:334–345.

- 487 Murphy ME, Miller BT, King JR. 1989. A structural comparison of fault bars with feather defects known to be
488 nutritionally induced. *Canadian Journal of Zoology* 67:1311–1317.
- 489 Negro JJ, Bildstein KL, Bird DM. 1994. Effects of food deprivation and handling stress on fault-bar formation in
490 nestling American Kestrels *Falco sparverius*. *Ardea* 82:263–267.
- 491 Newton I. 2007. Weather-related mass-mortality events in migrants. *Ibis* 149:453–467.
- 492 Nice MM. 1957. Nesting success in altricial birds. *The Auk* 74:305–321.
- 493 Norberg UM. 1990. *Vertebrate flight: mechanics, physiology, morphology, ecology and evolution*. Berlin, Germany:
494 Springer-Verlag.
- 495 Oelbermann K, Scheu S. 2002. Stable isotope enrichment ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) in a generalist predator (*Pardosa*
496 *lugubris*, Araneae: Lycosidae): effects of prey quality. *Oecologia* 130:337–344.
- 497 Oklahoma Climatological Survey. 2014. Average date of last freeze: 1981-2010.
498 http://climate.ok.gov/index.php/climate/map/average_date_of_last_freeze/oklahoma_south-central_u.s
- 499 Ortega KL, Smith TM, Manross KL, Kolodziej AG, Scharfenberg KA, Witt A, Gourley JJ. 2009. The Severe
500 Hazards Analysis and Verification Experiment. *Bulletin of the American Meteorological Society* 90:1519–
501 1530.
- 502 Pap PL, Barta Z, Tökölyi J, Vágási CI. 2007. Increase of feather quality during moult: a possible implication of
503 feather deformities in the evolution of partial moult in the Great Tit *Parus major*. *Journal of Avian Biology*
504 38:471–478.
- 505 Paritte JM, Kelly JF. 2009. Effect of cleaning regime on stable-isotope ratios of feathers in Japanese Quail (*Coturnix*
506 *japonica*). *The Auk* 126:165–174.
- 507 Polito MJ, Abel S, Tobias CR, Emslie SD. 2011. Dietary isotopic discrimination in gentoo penguin (*Pygoscelis*
508 *papua*) feathers. *Polar Biology* 34:1057–1063.
- 509 Post DM. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology*
510 83:703–718.
- 511 Prum RO, Williamson S. 2001. Theory of the growth and evolution of feather shape. *Journal of Experimental*
512 *Zoology* 291:30–57.
- 513 R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for Statistical
514 Computing, Vienna, Austria:<http://www.R-project.org>.
- 515 Rasband WS. 2014. ImageJ. <http://imagej.nih.gov/ij/>
- 516 Ricklefs RE. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9:1–48.
- 517 Riddle O. 1908. The genesis of fault-bars in feathers and the cause of alternation of light and dark fundamental bars.
518 *The Biological Bulletin* 14:328–371.
- 519 Rittenhouse CD, Pidgeon AM, Albright TP, Culbert PD, Clayton MK, Flather CH, Huang C, Masek JG, Radeloff
520 VC. 2010. Avifauna response to hurricanes: regional changes in community similarity. *Global Change Biology*
521 16:905–917.
- 522 Rohrbaugh RW, Reinking DL, Wolfe DH, Sherrod SK, Jenkins MA. 1999. Effects of prescribed burning and
523 grazing on nesting and reproductive success of three grassland Passerine species in tallgrass prairie. *Studies in*
524 *Avian Biology* 19:165–170.
- 525 Romano A, Rubolini D, Caprioli M, Boncoraglio G, Ambrosini R, Saino N. 2011. Sex-related effects of an immune
526 challenge on growth and begging behavior of Barn Swallow nestlings. *PLoS ONE* 6:e22805.
- 527 Sanpera C, Valladares S, Moreno R, Ruiz X, Jover L. 2008. Assessing the effects of the Prestige oil spill on the
528 European shag (*Phalacrocorax aristotelis*): trace elements and stable isotopes. *The Science of the Total*
529 *Environment* 407:242–9.
- 530 Sarasola JH, Jovani R. 2006. Risk of feather damage explains fault bar occurrence in a migrant hawk, the
531 Swainson's hawk *Buteo swainsoni*. *Journal of Avian Biology* 37:29–35.
- 532 Sears J, Hatch SA, O'Brien DM. 2009. Disentangling effects of growth and nutritional status on seabird stable
533 isotope ratios. *Oecologia* 159:41–8.
- 534 Serrano D, Jovani R. 2005. Adaptive fault bar distribution in a long-distance migratory, aerial forager passerine?
535 *Biological Journal of the Linnean Society* 85:455–461.

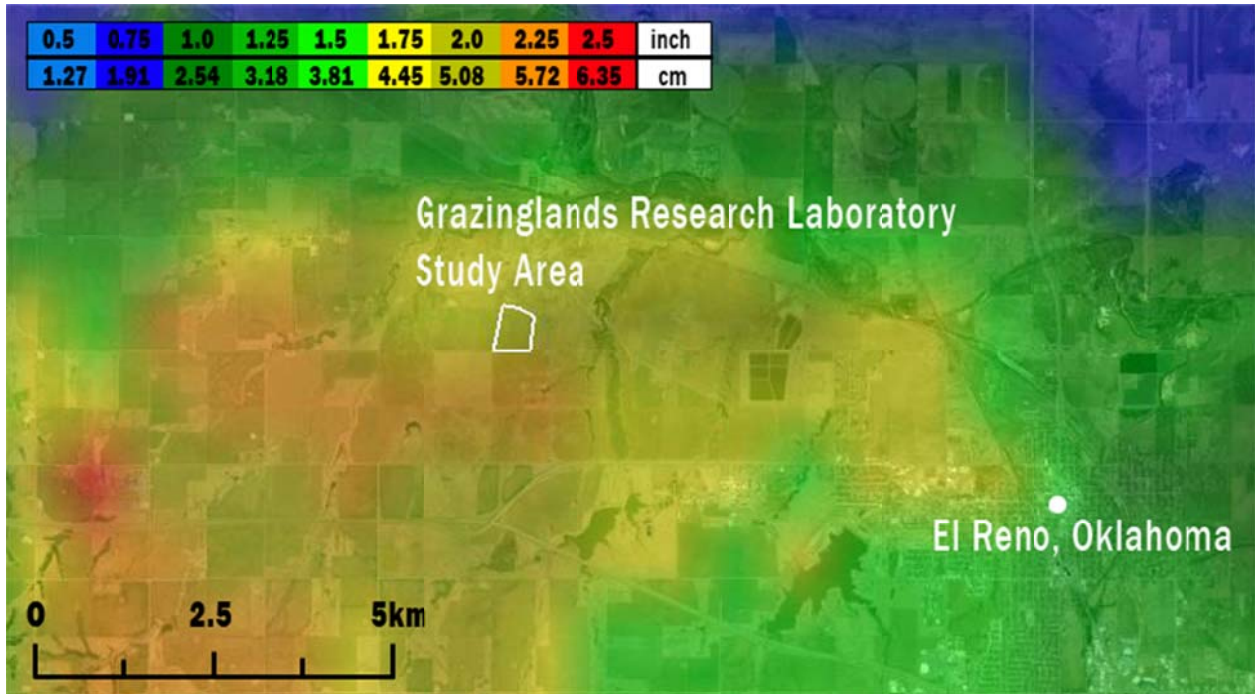
- 536 Shaw-Allen PL, Romanek CS, Bryan A. L., Brant H, Jagoe CH. 2005. Shifts in relative tissue $\delta^{15}\text{N}$ values in
537 Snowy Egret nestlings with dietary mercury exposure: a marker for increased protein degradation.
538 Environmental Science & Technology 39:4226–4233.
- 539 Sims CG, Holberton RL. 2000. Development of the corticosterone stress response in young Northern Mockingbirds
540 (*Mimus polyglottos*). General and Comparative Endocrinology 119:193–201.
- 541 Slagsvold T. 1982. Sex, size, and natural selection in the Hooded Crow *Corvus corone cornix*. Ornis Scandinavica
542 13:165–175.
- 543 Smith RL. 1963. Some ecological notes on the grasshopper sparrow. Wilson Bulletin 75:159–165.
- 544 Sockman KW, Schwabl H. 2001. Plasma corticosterone in nestling American Kestrels: effects of age, handling
545 stress, yolk androgens, and body condition. General and Comparative Endocrinology 122:205–12.
- 546 Sodhi NS. 2002. A comparison of bird communities of two fragmented and two continuous southeast Asian
547 rainforests. Biodiversity and Conservation 11:1105–1119.
- 548 Stumpf GJ, Smith TM, Hocker J. 2004. New hail diagnostic parameters derived by integrating multiple radars and
549 multiple sensors. In: Preprints, 22nd Conf. on Severe Local Storms, Hyannis, MA, Amer. Meteor. Soc. P.
- 550 Sutton GM. 1936. The postjuvinal molt of the Grasshopper Sparrow. Occasional Papers of the University of
551 Michigan Museum of Zoology 336:1–7.
- 552 Symes CT, Woodborne SM. 2011. Variation in carbon and nitrogen stable isotope ratios in flight feathers of a
553 moulting White-bellied Sunbird *Cinnyris talatala*. Ostrich 82:163–166.
- 554 Trapp RJ, Diffenbaugh NS, Brooks HE, Baldwin ME, Robinson ED, Pal JS. 2007. Changes in severe thunderstorm
555 environment frequency during the 21st century caused by anthropogenically enhanced global radiative forcing.
556 Proceedings of the National Academy of Sciences 104 :19719–19723.
- 557 Uccellini LW. 2014. May 2013 Oklahoma Tornadoes and Flash Flooding, National Oceanic and Atmospheric
558 Administration. Norman, OK.
- 559 Vickery PD. 1996. Grasshopper Sparrow (*Ammodramus savannarum*). In: Poole A, Gill RA eds. The Birds of North
560 America. Philadelphia, PA: The Birds of North America,.
- 561 Wada H, Hahn TP, Breuner CW. 2007. Development of stress reactivity in White-crowned Sparrow nestlings: total
562 corticosterone response increases with age, while free corticosterone response remains low. General and
563 Comparative Endocrinology 150:405–13.
- 564 Waterlow JC. 1968. The adaptation of protein metabolism to low protein intake. In: McCance RA, Widdowson EM
565 eds. Calorie and protein deficiencies. Boston, MA: Little & Brown, 61–72.
- 566 West JB, Bowen GJ, Cerling TE, Ehleringer JR. 2006. Stable isotopes as one of nature’s ecological recorders.
567 Trends in Ecology & Evolution 21:408–14.
- 568 Whitmore RC, Mosher JA, Frost HH. 1977. Spring migrant mortality during unseasonable weather. The Auk
569 94:778–781.
- 570 Wiley JW, Wunderle JM. 1993. The effects of hurricanes on birds, with special reference to Caribbean islands. Bird
571 Conservation International 3:319–349.
- 572 Williams CT, Buck CL, Sears J, Kitaysky AS. 2007. Effects of nutritional restriction on nitrogen and carbon stable
573 isotopes in growing seabirds. Oecologia 153:11–18.
- 574 Wingfield JC. 1988. Changes in reproductive function of free-living birds in direct response to environmental
575 perturbations. In: Processing of Environmental Information in Vertebrates. Springer, 121–148.
- 576 Wingfield JC. 2008. Comparative endocrinology, environment and global change. General and Comparative
577 Endocrinology 157:207–16.
- 578 Witt A, Eilts MD, Stumpf GJ, Johnson JT, Mitchell EDW, Thomas KW. 1998. An enhanced hail detection
579 algorithm for the WSR-88D. Weather and Forecasting 13:286–303.
- 580 Wood HB. 1950. Growth bars in feathers. The Auk 67:486–491.

581 Table 1: Clutch initiation phenology of 149 Grasshopper Sparrow nests at 20 sites in Washington and
 582 Osage Counties, Oklahoma. Expected status on May 31 was based upon a mean clutch size of 4,
 583 incubation initiated on the penultimate egg, and an 11-day incubation period (Vickery 1996).
 584

<i>Clutch Initiation Period</i>	<i>Likely Status on May 31</i>	<i>1992-96 Count</i>	<i>Proportion of Late-August</i>	
			<i>Fledged Juveniles*</i>	<i>Cumulative Proportion</i>
≤ May 4	Fledged	1	0.7	0.7
May 5-18	Nestlings	36	26.9	27.6
May 19-31	Eggs	37	27.6	55.2
Jun 1 - Jul 13	Pending ^{*,1}	60	44.8	100.0
> Jul 13	Pending ^{*,2}	15	n/a*	n/a*

*By the late-August sampling period the surviving young produced by "pending" clutches would have been either: (1) fully fledged and roaming; or (2) less likely to be capable of sustained flight or to have flocked with other juveniles (Vickery 1996)

585



586
587
588
589
590
591

Figure 1: Map of the study area (white outline) showing the maximum size of hailstones that fell across the region on May 31, 2013. Hailstone size was estimated from National Weather Service WSR-88D radar data using the Maximum Estimated Size of Hail model (MESH; Witt et al. 1998; Stumpf et al. 2004) and are displayed along a light blue (<0.5") to red (2.25 to 2.5") color scale.

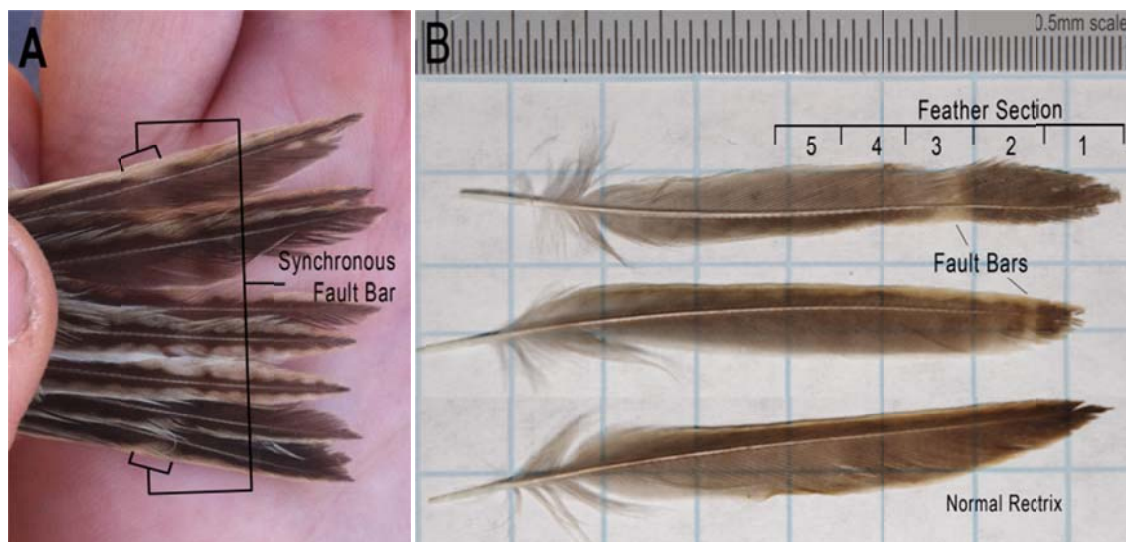
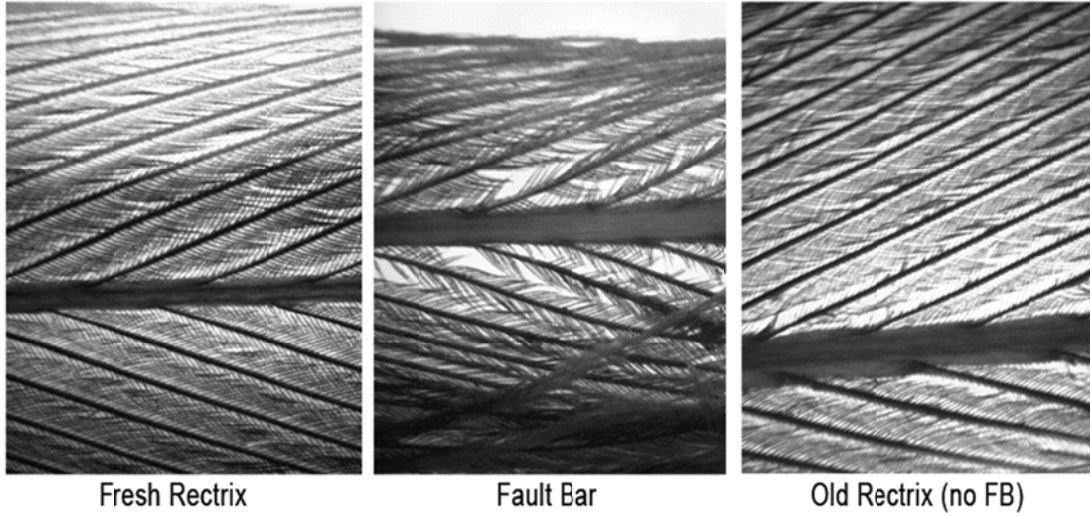
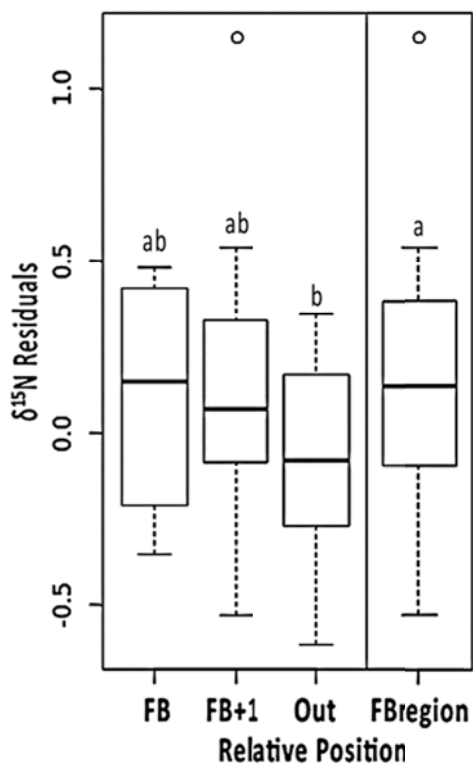
592
593
594
595
596
597

Figure 2: Photographs of Grasshopper Sparrow retrices from GRL. Panel A shows an individual tail with a synchronous band of fault bars. Panel B illustrates the sections sampled from the retrices of juvenile Grasshopper Sparrows. Sampling was constrained to provide a minimum of 0.2-0.3mg from each section. Shown are two examples of feathers with fault bars (top) and one of normal growth (bottom).



598
599
600
601
602

Figure 3: Backlit microscope views (20x) of Grasshopper Sparrow feather rachii and barbules in a fresh rectrix collected after post-juvenile molt (left), a rectrix with fault bar (middle), and a normal, worn juvenile feather (right).



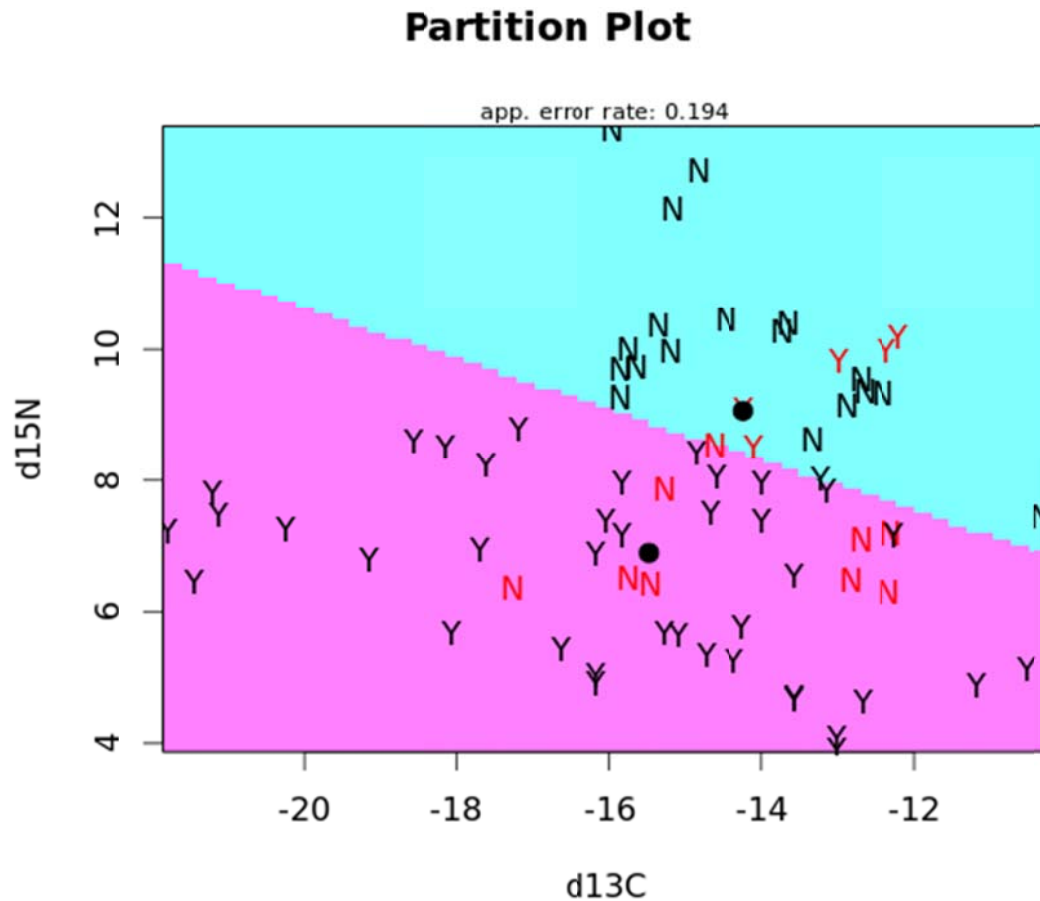
603
604
605
606
607
608

Figure 4: Distribution of $\delta^{15}\text{N}$ corrected for individual variation in slope and population-level patterns among sections of fault bar feathers. Shown are box plots of the data from sections containing fault bars (FB), immediately downstream from fault bars (FB+1), outside the fault bar region (Out) and pooled FB & FB+1 data (FBRegion). Significant groupings are designated by lowercase letters.

Supplemental Information

Supplemental Table S1: Nitrogen and carbon stable isotope fractionation within sections of juvenile GRSP rectrices. Sections were sequential samples of approximately equal weight taken from the tip (Section 1) proximally. Sections containing fault bars are highlighted with grey boxes. In three instances, the section sample was lost due to an error during the stable isotope analysis process (indicated as "Lost").

Individual (Band Number)	Fault Bar	Section 1		Section 2		Section 3		Section 4		Section 5		All Sections (mean±s.d.)	
		$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
1831-10723	No	9.71	-15.85	12.15	-15.18	12.73	-14.84	13.36	-15.95			11.98±1.60	-15.45±0.53
1831-10725	No	9.98	-15.21	10.46	-14.47	10.27	-13.73	10.40	-13.65			10.28±0.21	-14.26±0.73
1831-10736	No	9.72	-15.64	10.01	-15.74	10.37	-15.35	9.27	-15.87			9.84±0.47	-15.65±0.22
1831-10742	No	7.87	-15.29	<i>Lost</i>	<i>Lost</i>	9.14	-12.88	8.55	-14.63			8.52±0.63	-14.27±1.25
1831-10743	No	6.51	-12.83	7.21	-12.31	7.44	-10.33	7.11	-12.70			7.07±0.39	-12.04±1.16
1831-10745	No	6.39	-17.28	6.53	-15.75	6.33	-12.34	6.43	-15.46			6.42±0.09	-15.21±2.07
1831-10747	No	8.63	-13.33	9.33	-12.42	9.38	-12.65	9.55	-12.70			9.22±0.40	-12.78±0.39
Normal Feather:	Mean	8.40	-15.06	9.28	-14.31	9.38	-13.16	9.24	-14.42			9.07±1.94	-14.24±1.62
	s.d.	1.52	1.52	2.10	1.58	2.09	1.68	2.28	1.42				
1831-10714	Yes	7.17	-15.83	8.24	-17.62	8.52	-18.13	8.78	-17.19			8.18±0.71	-17.19±0.99
1831-10718	Yes	7.26	-20.25	6.81	-19.17	7.95	-15.82	7.51	-14.69	6.90	-16.17	7.29±0.47	-17.22±2.37
1831-10722	Yes	7.97	-13.99	8.01	-13.23	7.85	-13.16	7.17	-12.26			7.75±0.39	-13.16±0.71
1831-10724	Yes	8.61	-18.58	8.05	-14.60	8.50	-14.09	7.38	-14.00			8.13±0.56	-15.32±2.19
1831-10726	Yes	5.65	-15.11	5.03	-16.16	5.43	-16.65	5.66	-18.05			5.44±0.30	-16.49±1.22
1831-10734	Yes	6.96	-17.70	7.37	-16.05	8.42	-14.87	<i>Lost</i>	<i>Lost</i>			7.58±0.75	-16.21±1.42
1831-10735	Yes	6.48	-21.44	7.80	-21.20	7.22	-21.79	7.46	-21.12			7.24±0.56	-21.39±0.30
1831-10737	Yes	9.09	-14.22	10.19	-12.22	9.98	-12.37	9.81	-13.00			9.77±0.48	-12.95±0.91
1831-10738	Yes	4.92	-16.17	<i>Lost</i>	<i>Lost</i>	6.57	-13.57	4.71	-13.58	4.64	-12.68	5.21±0.91	-14.00±1.50
1831-10748	Yes	5.34	-14.72	5.67	-15.29	5.24	-14.36	5.76	-14.27			5.50±0.25	-14.66±0.46
1831-10749	Yes	3.92	-13.03	4.09	-13.02	5.14	-10.54	4.88	-11.19	4.66	-13.58	4.54±0.52	-12.27±1.32
Fault bar feather:	Mean	6.67	-16.46	7.13	-15.85	7.35	-15.03	6.91	-14.94	5.40	-14.14	6.91±1.63	-15.48±2.82
	s.d.	1.60	2.71	1.78	2.84	1.58	3.05	1.66	3.01	1.30	1.81		
All Individuals:	Mean	7.34	-15.91	7.93	-15.27	8.14	-14.30	7.87	-14.72	5.40	-14.14	7.72±2.03	-15.01±2.50
	s.d.	1.75	2.37	2.13	2.51	2.01	2.71	2.21	2.43	1.30	1.81		



Supplemental Figure S1: Partition plot of $\delta^{15}\text{N}$ versus $\delta^{13}\text{C}$ from sections analyzed within feathers containing fault bars (Y) and normal feathers (N). The dividing line was based upon a linear discriminant function analysis with jackknifed prediction calculated using the 'partimat' function in the R package klaR. Samples indicated in red font signify misassignments (19.4% of cases).



Supplemental Figure S2: Photograph of fault bars in the primary wing feathers of a juvenile Grasshopper Sparrow. Note that compared to the fault bars seen among rectrices these fault bars are narrower, do not show a loss in pigmentation, and are not synchronous. The tail of the same individual is pictured in Figure 2A.