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RH: LIFE-HISTORY EVOLUTION IN PRAIRIE CHICKENS—*McNew et al.*

EVIDENCE FOR HUMAN-MEDIATED LIFE-HISTORY EVOLUTION
IN GREATER PRAIRIE-CHICKENS

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29 ABSTRACT

30 Predation, food, climate and other environmental factors have a significant influence on
31 the evolution of vertebrate life history traits. Growing evidence indicates that human activities
32 can also affect evolutionary processes by a range of mechanisms, including impacts on life
33 history traits mediated by the effects of habitat management on survival of nests and adults. We
34 tested for anthropogenic effects on the life-history evolution of Greater Prairie-Chickens
35 (*Tympanuchus cupido*) breeding at three sites across a gradient of landscape alteration in eastern
36 Kansas, USA. Female prairie chickens breeding in an area heavily fragmented by rowcrop
37 agriculture and roads had low annual survival probabilities (0.15 ± 0.08 SE), and relatively high
38 survival of nests (0.16 ± 0.04) and broods (0.48 ± 0.12). In contrast, two populations breeding in
39 areas with large tracts of contiguous tallgrass prairie had high annual survival (0.37 ± 0.09 and
40 0.68 ± 0.09), and low survival of nests (0.07 ± 0.02 and 0.12 ± 0.03) and broods (0.29 ± 0.09 and
41 0.38 ± 0.09). Consistent with life-history theory, the population in the fragmented area with
42 higher adult mortality also had greater reproductive effort, and egg and clutch volumes were 5%
43 and 9% larger than at the other study areas. Reproductive effort was not influenced by other
44 explanatory variables, including residual female body mass. Overall, variation in the life history
45 traits of prairie chickens was most consistent with site differences in predation rates and
46 mortality of adult females. Impacts of predation on breeding females were apparently mediated
47 by the anthropogenic effects of road development and conversion of grasslands to cropland. Our
48 results indicate that land use and land cover change can alter the life history evolution of a short-
49 lived species at small spatial and short temporal scales. Future tests could examine changes in
50 life-history traits as part of translocation efforts for restoration of grouse populations.
51 *Key Words:* anthropogenic impacts, demography, evolution, grouse, reproduction, survival.

52 INTRODUCTION

53 Life-history theory predicts that the diversity of life-history strategies in vertebrates can
54 be explained by tradeoffs among demographic traits that maximize lifetime reproduction success
55 and fitness. Species with low adult survival should invest heavily in components of reproduction
56 whereas long-lived organisms should invest less in current reproduction, at least early in their
57 lives, to maximize benefits from residual reproductive value in future breeding attempts (Roff
58 1992, Martin 2002). Interspecific comparisons of variation in avian life history traits have
59 provided evidence for tradeoffs between annual survival and the components of reproductive
60 effort, including the probabilities of breeding and renesting, clutch size, and egg mass (Martin
61 1995, Ricklefs 2000, Sæther and Bakke 2000, Martin et al. 2006). Studies seeking ecological
62 correlates of patterns of avian life history variation have usually focused on four major
63 environmental factors: predation, food limitation, climatic conditions and duration of the
64 breeding season (Badyaev 1997, Conway and Martin 2000, Sandercock et al. 2005). Of these
65 four factors, predation may be the most important environmental factor explaining life history
66 variation within and among different species of birds because most demographic losses are
67 caused by predator activity (Ricklefs 1969, Martin 1995).

68 High rates of nest predation are predicted to favor reductions in reproductive effort
69 (Martin 2004). In songbirds, high levels of nest predation are associated with reductions in egg
70 size, clutch mass, and nest attentiveness, and increases in nestling growth rates (Conway and
71 Martin 2000, Fontaine and Martin 2006, Remeš and Martin 2002, Martin et al. 2006).
72 Reductions in reproductive effort may be mediated by tradeoffs among the different components
73 of fecundity if finite resources must be partitioned between the number and size of offspring
74 (Smith and Fretwell 1974, Winkler and Wallin 1987). Juvenile survival may place thresholds on

75 the minimum size of offspring, and large eggs tend to produce large chicks that have higher
76 survival rates in birds with precocial young (Myrberget 1977, Moss et al. 1981). Intraspecific
77 tradeoffs between clutch and egg size are rarely reported in birds, in part because egg size is
78 highly heritable (Christians 2002). Nevertheless, egg mass was negatively associated with clutch
79 size in an interspecific comparison of songbird demography (Martin et al. 2006), and also
80 increased in response to removals of nest predators (Fontaine and Martin 2006).

81 In contrast to the effects of nest predation, low rates of adult mortality are predicted to
82 favor reduced reproductive effort (Martin 2004). In songbirds, species with low adult mortality
83 exhibit reduced rates of nest attendance, and lower attentiveness is associated with longer
84 incubation periods (Martin 2002). Furthermore, songbird parents of species with low adult
85 mortality are more sensitive to predation risk when provisioning dependent offspring
86 (Ghalambor and Martin 2001). The effects of predators on juvenile survival may also play a
87 critical role in shaping avian life histories, with low rates of juvenile mortality favoring increased
88 reproductive effort (Russell 2000, Martin 2002). Life history studies that address juvenile
89 survival are fairly limited, primarily because of logistical difficulties in tracking and monitoring
90 mobile young during natal dispersal (Hannon and Martin 2006).

91 Comparative studies of grouse (Tetraoninae) have played an important role in the
92 development and testing of life history theory. Interspecific studies have demonstrated that
93 grouse exhibit the same fast-slow continuum in life-history strategies that is found in other
94 groups of vertebrates, including tradeoffs between clutch size and adult survival (Zammuto 1986,
95 Arnold 1988, Jönsson et al. 1991). At an intraspecific level, demographic studies of ptarmigan
96 (*Lagopus* spp.) have shown that alpine populations at southern latitudes have lower fecundity
97 and higher adult survival than arctic populations at northern latitudes, and that predation is

98 important as an environmental factor (Sandercock et al. 2005, Novoa et al. 2008). To date, most
99 studies of life-history evolution in birds have focused on the impacts of environmental factors
100 under natural conditions in undisturbed habitats. However, mounting evidence now indicates
101 that human activities can affect evolutionary processes through a variety of mechanisms,
102 including habitat modification, selective harvest, captive breeding, and translocations (Carroll et
103 al. 2007, Smith and Bernatchez 2008). Anthropogenic effects on land use and habitat
104 fragmentation have led to evolutionary change in the demographic traits of Lesser Prairie-
105 Chickens (*Tympanuchus pallidicinctus*, Patten et al. 2005). Historic differences in land tenure
106 created major differences in the extent of fencing, power lines and roads in rural areas of
107 Oklahoma and New Mexico. Collisions with fence lines are a major cause of mortality of female
108 prairie chickens in Oklahoma (Wolfe et al. 2007), and higher adult mortality has selected for
109 differences in life-history strategies because females in Oklahoma lay larger clutches and
110 produce more nesting attempts per year than females in New Mexico.

111 In this study, we compare the life-history traits of three independent populations of
112 Greater Prairie-Chickens (*T. cupido*) across a gradient of human landscape alteration in eastern
113 Kansas. If anthropogenic changes lead to rapid evolution of avian life history traits, we expected
114 that prairie grouse might be good candidates to investigate these effects because these species
115 have large clutch sizes, low adult survival, and presumably shorter generation times than tundra
116 or forest grouse (Patten 2009). We also expected that life-history changes might be mediated by
117 nest predation because Greater Prairie-Chickens exhibit considerable variation in nest survival
118 among different populations (0-72%) and predation is the primary cause of reproductive losses
119 (Schroeder and Robb 1993, Peterson and Silvy 1996). Finally, our analyses were strengthened
120 by use of standardized field protocols to investigate a suite of life history traits among multiple

121 populations of a single species with a shared evolutionary history. Our approach controls for
122 differences in methodology and phylogenetic relationships that can be an issue for interspecific
123 comparisons of life-history traits (Martin 1995, Sandercock et al. 2005, Martin et al. 2006).

124 STUDY SPECIES AND STUDY SITES

125 Greater Prairie-Chickens (hereafter ‘prairie chickens’) are endemic to the native
126 grasslands of the central United States. Prior to European settlement, prairie chickens were
127 distributed across all areas occupied by tallgrass prairie in North America (Schroeder and Robb
128 1993). Large-scale conversions of native prairies to rowcrop agriculture during the last century
129 are thought to be the major cause of declines in both the distribution and number of prairie
130 chickens, that have led to the deleterious effects of population bottlenecks (Johnson and Dunn
131 2008). The core of the extant range of prairie chickens occurs in eastern Kansas and adjacent
132 states (Schroeder and Robb 1993). In Kansas, prairie-chickens primarily occur in areas that are
133 dominated by native grasslands, such as the Flint Hills ecoregion. Nevertheless, prairie chickens
134 can tolerate moderate amounts of cultivated agriculture (<40% of total area), and populations of
135 prairie chickens are also found in the Smoky Hills ecoregion. Elsewhere, cultivation, grazing,
136 and other types of human land use have an impact on the population viability of prairie chickens,
137 but the potential role of land use and land cover change as drivers of evolutionary change have
138 not been investigated (Svedarsky et al. 2003).

139 Our study occurred at three discrete research areas; two sites located in the Flint Hills
140 (study areas 1 and 2) and one site in the Smoky Hills (study area 3). The three study sites
141 differed in landscape composition and pattern, as well as rangeland management practices.
142 Study area 1 (1,106 km²) was located in the southern Flint Hills, had landcover of 90% grassland
143 and 3% cropland, and a road density of 0.32 km of roads per km². The majority of the site was

144 burned annually in the spring, and managed with intensive early stocking (IESB, 1 head/0.8 ha
145 for 90 days; Smith and Owensby 1978, With et al. 2008). Study area 2 (671 km²) was located in
146 the north-central Flint Hills, had landcover of 81% grassland and 10% cropland, and a road
147 density of 0.57 km per km². Annual spring burning was common and lands were managed with
148 a mixture of IESB and season-long stock grazing (SLSB; 1 head/1.6 ha for 180 days). Study
149 area 3 (1,630 km²) was located in the Smoky Hills ecoregion and was more fragmented with
150 landcover of 53% grassland and 38% cropland, and a higher road density of 1.4 km per km².
151 Cultivated crops include sorghum, corn, wheat, and soybeans. Native grass pastures at study
152 area 3 were burned infrequently at fire return intervals >1 year, grazed at low intensity (1 head /
153 > 2 ha for 90 days), and cattle stocking occurred later in the season than at the other two study
154 sites. Landscape differences among our three study areas, combined with concurrent field
155 studies with standardized protocols, provided an opportunity to assess the potential evolution of
156 life-history strategies of prairie chickens in response to anthropogenic land use and land cover
157 change.

158 METHODS

159 FIELD METHODS

160 Prairie chickens were captured at lek sites during the spring with walk-in traps and drop-
161 nets (Silvy et al. 1990, Schroeder and Braun 1991). Captured birds were sexed by plumage
162 characteristics and size (Henderson et al. 1967). We determined age-class as yearling or adult
163 from the shape, coloration and wear of the outermost two primaries (numbers 9 and 10;
164 Schroeder and Robb 1993). Morphometrics of adults, including total mass and length of the
165 tarsus-metatarsus, were measured at the time of capture. All birds were individually marked
166 with color leg bands and females were fitted with 11-g necklace-style VHF radio transmitters,

167 equipped with mortality switches and an expected battery life of 12 months (Model RI-2B,
168 Holohil Systems Ltd., Ontario, Canada). Radio-marked hens were monitored ≥ 3 times/week
169 from project trucks during the nesting and brood-rearing period (Apr-Aug) and ≥ 1 time per week
170 during the rest of the year (Sep-Mar). Once a female had localized in an area for three
171 successive days, we used a portable radio receiver and handheld Yagi antenna to locate the
172 incubating female. We flushed the female once in early incubation to count the eggs, to
173 determine the stage of incubation, and to record the nest location. Females with nests were
174 monitored daily at a distance by triangulation of the radio signal. Once it was determined that
175 the female was no longer tending the nest, we classified nest fate as successful (≥ 1 chick
176 produced), failed, depredated, or abandoned.

177 BODY MASS OF FEMALES

178 Reproductive effort of female prairie chickens at the different research areas could be
179 influenced by site differences in food resources if females with heavier body mass are in better
180 nutritional condition and lay larger eggs. Alternatively, site differences in body mass could be a
181 result of seasonal differences in ovarian development among females at capture. We evaluated
182 the first possibility by regressing female mass at capture on length of the tarsus-metatarsus as an
183 index of body size. Residual body mass of females was used as an index of nutritional condition
184 in the spring before egg-laying. Assessment of ovarian development was difficult because we
185 were unable to determine if females were gravid at capture. We used the interval between the
186 day of capture and the day of nest initiation as a covariate (McNew et al., unpubl. ms). Mass of
187 female grouse may increase before the onset of egg-laying (Hannon and Roland 1984), and we
188 expected that females with shorter intervals between capture and nest initiation were more likely
189 to be gravid. We used analysis of covariance to test whether regional differences in female mass

190 at capture were influenced by the length of time between capture and nest initiation. We tested
191 factorial models with main effects and interaction terms, and all parametric statistics were
192 calculated using procedures of Program SAS (ver. 9.1, SAS Institute, Cary, NC).

193 CLUTCH SIZE AND EGG VOLUME

194 Clutch size was calculated as the maximum number of eggs recorded per clutch once
195 egg-laying was completed and a female had started incubation. We measured egg volume for
196 first nests with ≥ 10 eggs and renests with ≥ 9 eggs. Eggs were temporarily collected and length
197 (L) and breadth (B) measured to the nearest 0.1 mm using calipers. Linear measurements were
198 converted to an estimated egg volume (V) with the following equation (Narushin 2005):

$$199 \quad V = (0.6057 - 0.0018B)LB^2$$

200 Mean clutch size and egg volumes were compared among research areas using analysis of
201 variance. We also compared egg volume and clutch size relative to residual body mass of
202 females. Analysis of covariance was used to test whether site differences in clutch size and egg
203 volume could be explained by potential variation in the nutritional condition of females.

204 NEST SURVIVAL AND BROOD SURVIVAL

205 Nest survival is the probability of a nest producing ≥ 1 hatched chick, whereas brood
206 survival was defined as the probability that ≥ 1 chick survives to fledging at 14 days after
207 hatching. We calculated daily rates of nest and brood survival for each study area with the nest
208 survival model of Program Mark (ver. 4.3, White and Burnham 1999, Dinsmore et al. 2002).
209 Multiple model selection and inference was used to evaluate the importance of environmental
210 factors on daily nest survival (Burnham and Anderson 1998). The three factors included in the
211 global model for nest survival included: nesting attempt (first or renest), female age, and research
212 area. We estimated a corrected probability of nest survival by extrapolating the daily nest

213 survival to an exponent equal to duration of the nesting cycle. Duration of the nesting cycle was
214 calculated assuming an egg-laying rate of one egg per day and an average incubation period of
215 25 d (McNew et al., unpubl. ms). To estimate brood survival prior to fledging, we used
216 systematic flush counts of females attending broods (Hubbard et al. 1999, Fields et al. 2006).
217 The probability of brood survival was calculated by extrapolating estimates of daily brood
218 survival over a 14 d period from hatching until fledging. Variances of derived parameters were
219 calculated using the delta method (Powell 2007).

220 ANNUAL SURVIVAL OF FEMALES

221 We estimated weekly survival of female prairie chickens during a 1-year period between
222 March 2007 and March 2008 with the nest survival procedure of Program Mark. The nest
223 survival model is a general procedure for known-fate data and is useful for estimating survival of
224 radio-marked birds (Hartke et al. 2006, Mong and Sandercock 2007). We used the most
225 parsimonious models to derive parameter estimates, and then extrapolated annual survival rates
226 at each research area as the product of weekly survival rates during the entire study period.

227 RESULTS

228 BODY MASS OF FEMALES

229 A total of 162 female prairie chickens were captured before egg-laying at our study areas
230 in eastern Kansas. Analysis of covariance showed there was no interaction between the effects
231 of study area and the interval between capture and egg-laying ($F_{2,153} = 0.34, P = 0.71$). Body
232 mass of female prairie chickens differed significantly among the three research areas ($F_{2,153} =$
233 $6.8, P = 0.001$), and females were heaviest at study area 3 (929 g), intermediate at study area 2
234 (908 g), and lightest at study area 1 (879 g, Table 1). The interval between capture and egg-
235 laying had a weak positive effect on female mass ($F_{1,153} = 2.9, P < 0.08$), but this factor had only

236 21% of the explanatory power of the effect of study area. We found no significant relationship
237 between female mass and tarsus-metatarsus length ($r^2 < 0.01$, $df = 1$, $P = 0.64$).

238 CLUTCH SIZE AND EGG VOLUME

239 Analysis of variance showed there was no interaction between the effects of study area or
240 nesting attempt on clutch size ($F_{2,151} = 0.06$, $P = 0.94$). First nests were consistently larger than
241 renests ($F_{1,151} = 34.2$, $P < 0.001$), and the number of eggs per clutch averaged 12.5 to 13.1 eggs
242 for first nesting attempts and 10.2 to 10.9 eggs for renests (Table 1). First nests at study area 3
243 tended to be larger by about 0.5 eggs per clutch, but overall, clutch size not differ significantly
244 among study areas ($F_{2,151} = 0.33$, $P = 0.72$). Analysis of covariance showed that was no
245 interaction between the effects of residual female mass and study area on egg volume ($F_{2,147} =$
246 1.14 , $P = 0.32$). Egg volume differed among the three study areas ($F_{5,147} = 2.3$, $P = 0.05$), with
247 the largest eggs laid at study area 3 (24.7 ml) and the smallest eggs at study area 1 (23.7 ml,
248 Table 1). Residual female condition did not explain variation in egg volume ($F_{2,147} = 1.1$, $P =$
249 0.32), and egg volume was not related to clutch size ($r^2 = 0.01$, $P = 0.17$).

250 NEST SURVIVAL AND BROOD SURVIVAL

251 During the breeding seasons of 2006-08, 231 nests of 206 female prairie chickens were
252 located and monitored, of which 44 were successful, for an apparent nest success rate of 19%.
253 Nest survival was modeled for a 103-day nesting period from 23 April to 19 July. The most
254 parsimonious model ($\Delta AIC_c = 0$) included a group effect for study area. Models where nest
255 survival varied among study areas were 9.9 times more likely than models where nest survival
256 was constant ($w_i/w_j = 0.79/0.08$). Variation in survival among study areas accounted for 79% of
257 the relative support of the data. Nest survival was lower at study area 1 (0.07 ± 0.02) compared
258 to the study areas 2 (0.12 ± 0.03) and 3 (0.16 ± 0.04 , Table 1). Overall nest survival for all sites

259 and nesting attempts combined was $0.12 \pm 0.04SE$. Evidence at failed nests indicated that
260 predation was the primary cause of nest mortality; accounting for 94% of all losses.

261 Forty-three broods were monitored from hatch until fledging at 14-d old. Brood survival
262 during this period was modeled for a 69-day brood-rearing period from 17 May to 24 July. A
263 model that contained an effect of study area was considered parsimonious ($\Delta AIC_c = 0.37$).
264 Models where brood survival varied among study areas had 44% of the relative support. Site
265 differences in brood survival were opposite to patterns of nest survival: survival of broods was
266 highest at study area 3 (0.45 ± 0.11), intermediate at study area 2 (0.32 ± 0.12), and lowest at
267 study area 1 (0.24 ± 0.10 , Table 1). Overall, the model-averaged estimate of brood survival until
268 fledging across all study areas was 0.35 ± 0.07 .

269 FEMALE ANNUAL SURVIVAL

270 Model selection based on AIC_c indicated that survival of female prairie chickens differed
271 among study areas. In fact, variation in survival among study areas was strongly supported by
272 the data, accounting for more than 99% of the relative support. Annual survival was greater at
273 study area 1 (0.68 ± 0.09) than at study areas 2 (0.37 ± 0.09) and 3 (0.15 ± 0.08 ; Table 1).
274 Overall annual survival of females during the 52-week period from March to February for all
275 sites pooled was $0.43 (\pm 0.06)$.

276 DISCUSSION

277 Female Greater Prairie-Chickens breeding at three sites across a gradient of
278 environmental conditions in the Flint Hills and Smoky Hills of eastern Kansas exhibited
279 variation in a suite of eight life-history traits. Females breeding at a study area consisting of
280 large, contiguous blocks of native prairie (study area 1) had the lightest body mass, laid the
281 smallest eggs, and had the lowest clutch volume. Nest and brood survival were low but annual

282 survival was high for prairie chickens breeding in large tracts of contiguous prairie. In contrast,
283 females breeding at a highly fragmented site (study area 3) had the heaviest body mass, laid the
284 largest eggs, and had the greatest clutch volume. The fragmented site had the highest rates of
285 nest and brood survival, although our estimates were depressed compared to values compiled for
286 other populations (Peterson and Silvy 1996). In fact, our estimates of annual survival for
287 females at the fragmented site are among the lowest values ever reported for a field study of
288 prairie chickens. Study area 2 in the Flint Hills had moderate amounts of habitat fragmentation
289 and the demographic parameters of female prairie chickens were intermediate as well. We
290 evaluate the potential roles of phenotypic plasticity and evolutionary processes as potential
291 explanations for the results of our demographic analyses.

292 Tradeoffs between realized fecundity and annual survival are often interpreted as
293 resulting from evolutionary processes, but tradeoffs can also be produced by phenotypic
294 plasticity and density-dependent competition (Ricklefs 2000). For example, site differences in
295 female mass in our study could have been an artifact of differences in date of capture and the
296 degree of gravidity among females before egg-laying. Timing of lek attendance did not differ
297 among the three study areas but nest initiation was delayed at study area 1, and females at study
298 area 3 could have been more gravid at capture (McNew et al., unpubl. ms). However, we reject
299 differences in seasonal phenology as an explanation for variation in female mass at capture,
300 because body mass was only weakly related to the interval between capture and date of nest
301 initiation, and still differed among areas after adjustment for the covariate.

302 Phenotypic plasticity could also be relevant if site differences in body mass, clutch size
303 and egg volume were due to regional differences in food availability that impacted the nutritional
304 body condition of egg-laying females. Females had the highest body mass, and laid the largest

305 clutches and eggs at study area 3, a site fragmented by agricultural development. Cultivated
306 agricultural fields comprised a higher proportion of the landscape at study area 3 and prairie
307 chickens will utilize grain sorghum and other crops during winter and early spring (Robel et al.
308 1970). Two lines of evidence suggest that nutritional condition cannot explain regional variation
309 in reproductive effort of prairie chickens in eastern Kansas. First, residual female mass did not
310 explain variation in egg volume among our three study areas. Food supplementation usually has
311 little impact on egg size of birds, but has larger effects on timing of laying and clutch size
312 (Christians 2002). Estimates of heritability for egg size are often high in birds, suggesting that
313 egg size may be under selective pressures unrelated to the nutritional status of laying females.
314 Second, egg volume of prairie chickens was not related to clutch size. Life-history theory
315 predicts a negative relationship between egg size and clutch size if female resources must be
316 partitioned (Roff 1992), but a positive association would be expected if both traits are impacted
317 by nutritional condition, which we did not observe.

318 Low reproductive effort among prairie chickens breeding in contiguous grasslands in
319 eastern Kansas was consistent with life-history theory, which predicts that high nest predation
320 and low adult mortality should select for reductions in reproductive effort (Roff 1992). Mortality
321 of female prairie chickens was almost entirely the result of predation (90%; L.B. McNew,
322 unpubl. data), with coyotes (*Canis latrans*) suspected in >60% of predation events. Thus, the
323 most important environmental factor leading to divergence in the life-history traits of prairie
324 chickens appears to be the impacts of predators on the survival of adults and nests. We lacked
325 estimates of predator abundance for our three study areas but study area 3 was clearly
326 fragmented by agricultural development and had a higher density of roads. Known predators of
327 prairie chickens, such as coyotes, use edge habitats and roads for travel and foraging (Kuehl and

328 Clark 2002, Tigas et al. 2002). Thus, anthropogenic changes in land use and habitat
329 fragmentation may have led to differential rates of exposure to predators. From our
330 observations, we conclude that the direct effects of human activities on grassland ecosystems,
331 and the indirect impacts of habitat modification upon predator-prey interactions have apparently
332 influenced the life-history evolution of Greater Prairie-Chickens in eastern Kansas during the last
333 century.

334 There is mounting evidence that human activities have led to ecologically significant
335 evolutionary change in a variety of taxa, and at range of temporal and spatial scales, contributing
336 to growing interest in the study of contemporary evolution (Carroll et al. 2007, Smith and
337 Bernatchez 2008). Relatively few studies have evaluated the impacts of habitat loss and
338 degradation on the life-history evolution of terrestrial vertebrates. Cutting of grasslands for hay
339 production destroys nests of grassland songbirds, including Savannah Sparrows (*Passerculus*
340 *sandwichensis*) breeding in dairy pastures in Vermont. Perlut et al. (2008) showed that timing of
341 hay cutting altered mating strategies and the occurrence of extra-pair copulations, as well as the
342 strength of selection on morphological traits. Fencing of pastures for livestock is a landscape
343 modification that poses a risk of collision mortality for female Lesser Prairie-Chickens (Wolfe et
344 al. 2007), and Patten et al. (2005) showed that female prairie chickens subject to higher fence
345 collision mortality laid larger clutches and had a greater probability of renesting than birds at less
346 heavily fenced sites. Our study extends these previous results by showing that landscape
347 modification by humans may lead to differential rates of predation that affect the life-history
348 traits of Greater Prairie-Chickens. Mammalian predators play an important role in structuring
349 terrestrial ecosystems (Pace et al. 1999), but previous studies investigating trophic dynamics
350 have primarily focused on the ecological consequences of the removal of top predators and

351 mesopredator release (Elmhagen and Rushton 2007, Berger et al. 2008). Changes in predator
352 abundance and diversity can also drive evolutionary change in the life-history strategies in lower
353 trophic levels. For example, predators can determine the life-history evolution of guppies
354 (*Poecilia reticulata*) in captivity and natural environments (Reznick et al. 2008). Selective
355 removal of top predators is one way that humans influence life-history evolution, but our results
356 suggest that indirect effects of landscape modification on predation risk can also be important.

357 Our project is one of the first studies to assess the influence of human landscape
358 alteration on the life-history evolution of grouse, and our work could be extended in two ways.
359 First, we observed the impacts of predation on the demographic parameters of prairie chickens
360 but were unable to determine whether variation in predation rates were due to a numerical or a
361 functional response. We did not attempt to estimate predator abundance, and the identity of
362 major predators was surmised by inspecting the remains of depredated nests and carcasses. Our
363 analyses would be informed by a better understanding of predator abundance and activity in
364 relation to land use and land cover changes. Second, our analyses were based on retrospective
365 comparisons of demographic data for prairie chickens at three study sites, and life-history traits
366 could have covaried with an environmental factor that we failed to consider (Ricklefs 2000).
367 Experimental protocols are a stronger approach to testing for local adaptation but would require
368 raising birds in a common environment or reciprocal transplants among different populations
369 (James 1983, Rhymer 1992, Bears et al. 2008). Experimental tests will be logistically difficult
370 for prairie chickens because of their large home range requirements, vagility and conservation
371 status. Wildlife management activities are rarely considered from an evolutionary perspective
372 but could have potential for analyses of contemporary life-history evolution in prairie chickens.
373 For example, comparisons of performance between wild prairie chickens and pen-reared

374 Attwater's Prairie-Chickens (*T.c. attwateri*) might yield insights into the selection conditions of
375 captive-rearing environments (Peterson and Silvy 1996, Hess et al. 2005). Finally, ongoing
376 translocations of prairie chickens from Kansas to relict populations in Illinois and Missouri
377 (Westemeier et al. 1998, J.C. Pitman, Kansas Department of Wildlife and Parks, pers. comm.)
378 will provide future opportunities for investigating adaptation in wild populations in new
379 environments.

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Table 1. Mean estimates (\pm SE) for life-history traits of female Greater Prairie-Chickens breeding at three study areas in eastern Kansas, 2006-08. Statistical analyses are described in text.

Parameter	Area 1	n	Area 2	n	Area 3	n	Statistics ^a
Body mass of females (g)	879 (7.9)	61	908 (8.7)	51	929 (8.8)	50	$F = 6.8, P < 0.01$
Clutch size of first nests	12.5 (0.3)	41	12.6 (0.3)	43	13.1 (0.3)	40	$F = 1.6, P = 0.21$
Clutch size of renests	10.4 (0.4)	21	10.9 (0.5)	14	10.2 (0.5)	10	$F = 0.5, P = 0.62$
Egg volume (ml)	23.7 (0.2)	62	24.2 (0.2)	58	24.7 (0.2)	51	$F = 2.3, P = 0.05$
Clutch volume (ml)	278 (6.8)	62	290 (7.1)	58	304 (7.5)	51	$F = 2.8, P = 0.06$
Nest survival	0.07 (0.02)	83	0.12 (0.03)	85	0.16 (0.04)	63	$\Delta AIC_c = 0.0, w_i/w_j = 7.3^a$
Brood survival	0.29 (0.09)	15	0.38 (0.09)	12	0.48 (0.12)	16	$\Delta AIC_c = 0.37, w_i/w_j = 1.2^a$
Annual survival of females	0.68 (0.09)	43	0.37 (0.09)	41	0.15 (0.08)	22	$\Delta AIC_c = 0.0, w_i/w_j = 99.0^a$

^a Parametric statistics were based on analysis of variance. Analyses of survival were based on model selection with AIC_c , where ΔAIC_c = difference in AIC_c between a model where survival differs among the three study areas and the minimum AIC_c model, and w_i/w_j = evidence ratios calculated as the ratio of relative support for the pooled weights of models where survival rates differed among the three study areas versus models where survival did not differ among areas.