Human-Mediated Selection on Life-History Traits of Greater Prairie-Chickens

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Abstract. Predation, food, climate, and other environmental factors have a significant influence on selection processes and evolution of vertebrate life-history traits. Growing evidence indicates that human activities can also affect evolutionary processes by a range of mechanisms, including impacts on life-history traits mediated by the effects of habitat management on survival of nests and adults. We tested for anthropogenic effects on the life-history evolution of Greater Prairie-Chickens (*Tympanuchus cupido*) breeding at three sites across a gradient of landscape alteration in eastern Kansas. Female prairie chickens breeding in an area heavily fragmented by row-crop agriculture and roads had low annual survival probabilities (0.32 ± 0.001 SE) and higher survival of nests (0.16 ± 0.04) and broods (0.48 ± 0.12) than the other two study areas. In contrast, two populations breeding in areas with large tracts of contiguous heavily grazed tallgrass prairie had higher annual survival (0.47 ± 0.002 and 0.68 ± 0.01) and lower survival of nests (0.07 ± 0.02 and 0.12 ± 0.03) and broods (0.29 ± 0.09 and 0.38 ± 0.09, respectively). Consistent with life-history theory predictions, the population in the fragmented area with higher adult mortality also had greater reproductive effort, and egg and clutch volumes were 5% and 9% larger than at the other study areas. Reproductive effort was not influenced by other explanatory variables, including residual female body mass. Overall, variation in the life-history traits of prairie chickens was most consistent with site differences in nest predation rates and mortality of adult females. Predation on breeding females was positively associated with the anthropogenic effects of road development and conversion of grasslands to cropland. Our results indicate that land use and land cover change can influence selection on life-history traits for a short-lived species at small spatial and short temporal scales, even after adjusting for potential phenotypic plasticity.

Key Words: anthropogenic impacts, demography, evolution, grouse, reproduction, survival.

life-history theory predicts that the diversity of life-history strategies in vertebrates can be explained by trade-offs among demographic traits that maximize lifetime reproductive success and fitness. Species with low adult survival should invest heavily in components of reproduction, whereas longer-lived organisms should invest less in current reproduction, at least early in their lives, to maximize benefits from residual reproductive value in future breeding attempts (Roff 1992, Martin 2002). Interspecific comparisons of variation in avian life-history traits have provided evidence for trade-offs between annual survival and the components of reproductive effort, including the probabilities of breeding and renesting, clutch size, and egg mass (Martin 1995, Ricklefs 2000, Sæther and Bakke 2000, Martin et al. 2006). Studies seeking ecological correlates of patterns of avian life-history variation have usually focused on four major factors: predation, food limitation, climatic conditions, and duration of the breeding season (Badyaev 1997, Conway and Martin 2000, Sandercock et al. 2005). Of these four factors, predation may be most important for explaining life-history variation within and among different species of birds because most demographic losses are caused by predator activity (Ricklefs 1969, 2008; Martin 1995).

High rates of nest predation are predicted to favor reductions in reproductive effort (Martin 2004). In songbirds, high levels of nest predation are associated with reductions in egg size, clutch mass, and nest attentiveness, and increases in nestling growth rates (Conway and Martin 2000, Remeš and Martin 2002, Fontaine and Martin 2006, Martin et al. 2006). Reductions in reproductive effort may be mediated by trade-offs among the different components of fecundity if finite resources must be partitioned between the number and size of offspring (Smith and Fretwell 1974, Winkler and Wallin 1987). Juvenile survival may place thresholds on the minimum size of offspring, and large eggs tend to produce large chicks that have higher survival rates in birds with precocial young (Myrberget 1977, Moss et al. 1981). Intraspecific trade-offs between clutch and egg size are rarely observed in birds, in part because egg size is highly heritable (Christians 2002). Nevertheless, egg mass decreased with increased clutch size in an interspecific comparison of songbird demography (Martin et al. 2006), and egg mass

increased in response to removals of nest predators (Fontaine and Martin 2006).

In contrast to the effects of nest predation, low rates of adult mortality are predicted to favor reduced reproductive effort (Martin 2004). In songbirds, species with low adult mortality exhibit reduced rates of nest attendance, and lower attentiveness is associated with longer incubation periods (Martin 2002). Trade-offs between survival and reproductive effort have been documented for precocial species as well, with females that have lower annual survival laying larger clutches (Patten et al. 2007) or exhibiting a higher propensity to renest (Martin et al., this volume, chapter 17). The effects of predators on juvenile survival may also play a critical role in shaping avian life histories, with low rates of juvenile mortality favoring increased reproductive effort (Russell 2000, Martin 2002). Life-history studies that address juvenile survival are fairly limited, primarily because of logistical difficulties in tracking and monitoring mobile young during natal dispersal (Hannon and Martin 2006).

Differences in resource acquisition among females can confound the detection of life-history trade-offs if life-history traits are phenotypically plastic (van Noordwijk and de Jong 1986). Trade-offs between realized fecundity and annual survival can be produced by resource limitations (Ricklefs 2000). For example, clutch size, nesting propensity, and the interval between nesting attempts were associated with the spring body condition of female Mallards (*Anas platyrhynchos*; Devries et al. 2008), and plasma protein and female age were significant predictors of renesting probability in Greater Sage-Grouse (*Centrocercus urophasianus*; Gregg et al. 2006). In addition, egg size has been found to vary among species in relation to residual body mass, an index of condition (Rahn et al. 1985, Sæther 1987). Indeed, the positive relationships between food resources and clutch and egg size have been invoked often to explain observations that do not support the clutch size:egg mass trade-off (Lack 1968, Sæther 1987, Martin et al., this volume, chapter 17).

Comparative studies of grouse (Tetraoninae) have played an important role in the development and testing of life-history theory. Interspecific studies have demonstrated that grouse exhibit the same fast–slow continuum in life-history strategies that is found in other groups of vertebrates, including trade-offs between clutch size and adult

survival (Zammuto 1986, Arnold 1988, Jönsson et al. 1991). Demographic studies of ptarmigan (*Lagopus* spp.) have shown that alpine populations at southern latitudes have lower fecundity and higher adult survival than arctic populations at northern latitudes, and that predation is important as an environmental factor (Sandercock et al. 2005, Novoa et al. 2008). To date, most studies of life-history variation in birds have focused on the impacts of environmental factors under relatively undisturbed or natural conditions (Bears et al. 2009, Martin et al. 2009, Martin et al., this volume, chapter 17). However, mounting evidence now indicates that human activities can affect evolutionary processes through a variety of mechanisms, including habitat modification, selective harvest, captive breeding, and translocations (Carroll et al. 2007, Smith and Bernatchez 2008). Anthropogenic effects on land use and habitat fragmentation may have led to the observed changes in the demographic traits of Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*; Patten et al. 2005). Historic differences in land tenure created major differences in the extent of fencing, power lines, and roads in rural areas of Oklahoma and New Mexico. Collisions with fences are a major cause of mortality of female prairie chickens in Oklahoma (Wolfe et al. 2007), and higher adult mortality due to collisions was correlated with larger clutch sizes and higher renesting rates in Oklahoma as compared to New Mexico (Patten et al. 2005). However, the indirect impacts of nest failure and adult mortality due to human-caused habitat alteration on the selection for demographic traits have not been assessed.

In this study, we compare the demographic traits of three independent populations of Greater Prairie-Chickens across a gradient of human landscape alteration. The landscapes of Kansas provide a unique opportunity to evaluate whether alteration of habitats impacts the selection of life-history traits of Greater Prairie-Chickens (*T. cupido*) because land use and range management practices vary significantly within the state. In the Flint Hills, large contiguous tracts of grassland are intensively managed for cattle production, whereas in the Smoky Hills, smaller tracts of less heavily grazed grassland are fragmented by row-crop agriculture (McNew et al., this volume, chapter 15). Habitat conditions impact the seasonal availability of lekking, nesting, and brood-rearing habitat (Patten et al. 2007), the phenology of breeding events (McNew et al., this volume, chapter 15), and variation in reproductive success and survival (McKee et al. 1998, Matthews et al., this volume, chapter 13). If anthropogenic changes lead to rapid selection for avian life-history traits, we expected that Greater Prairie-Chickens might be good candidates to investigate these effects because this species has large clutch sizes, low adult survival, and presumably shorter generation times than tundra or forest grouse (Patten 2009). We also expected that changes in vital rates might be mediated by nest predation because Greater Prairie-Chickens experience considerable variation in nest survival among different populations (0–72%), and nest predation is the primary cause of reproductive losses (Schroeder and Robb 1993, Peterson and Silvy 1996). If large variations in habitat conditions influence demographic rates, we expected greater reproductive effort in populations experiencing higher reproductive success or lower adult survival. Finally, our analyses were strengthened by use of standardized field protocols to investigate a suite of demographic traits among multiple populations of a single species. Our approach controls for differences in methodology and phylogenetic relationships that can be an issue for interspecific comparisons of life-history traits (Martin 1995, Sandercock et al. 2005, Martin et al. 2006).

STUDY SPECIES AND STUDY SITES

Greater Prairie-Chickens (hereafter prairie chickens) are endemic to the native grasslands of the central United States. Prior to European settlement, prairie chickens were distributed across all areas occupied by tallgrass prairie in North America (Schroeder and Robb 1993). Large-scale conversions of native prairies to row-crop agriculture during the last century are thought to be the major cause of declines in both the distribution and number of prairie chickens, which have led to population bottlenecks (Westemeier et al. 1998, Johnson and Dunn 2008). The core of the extant range of prairie chickens occurs in Kansas and adjacent states (Schroeder and Robb 1993). In Kansas, prairie chickens primarily occur in areas that are dominated by native grasslands, such as the Flint Hills ecoregion. Nevertheless, prairie chickens can tolerate moderate amounts of cultivated agriculture (<40% of total area), and populations of prairie chickens are also found in

more developed regions of Kansas. Elsewhere, cultivation, grazing, and other types of human land use have reduced the population viability of prairie chickens, but the potential role of land use and land cover change as drivers of natural selection have not been investigated (Svedarsky et al. 2003).

Our study occurred at three discrete study sites: two sites located in the southern and northern Flint Hills (South and North, respectively) and one site in the Smoky Hills (Smoky). The three study areas were ≥112 km apart and differed in landscape composition and pattern as well as rangeland management practices (McNew et al., this volume, chapter 15). The South site (635 km^2) had landcover of 90% grassland and 3% cropland, a mean grassland patch size of 185 ha, and a road density of 0.32 km of roads per km^2. The majority of the site was managed with range management practice of intensive early stocking and burned annually each spring (IESB, 1 head/0.8 ha for 90 days; Smith and Owensby 1978, With et al. 2008). The North site (533 km^2) had landcover of 81% grassland and 10% cropland, a mean grassland patch size of 51 ha, and a road density of 0.57 km per km^2. Annual spring burning was common and lands were managed with a mixture of IESB and season-long stock grazing and annual burning (SLSB; 1 head/1.6 ha for 180 days). The Smoky site (1,295 km^2) was more fragmented, with landcover of 53% grassland and 38% cropland, a mean grassland patch size of 15 ha, and a higher road density of 1.4 km per km^2. Cultivated crops include sorghum, corn, wheat, and soybeans. Native grass pastures at study area 3 were burned infrequently at fire return intervals >1 year, grazed at low intensity (1 head/>2 ha for 90 days), and cattle stocking occurred later in the season than at the other two study sites. Indices of prairie chicken densities for years of study, calculated as: mean number of prairie-chickens per lek × number of leks per study area size, were 0.10, 0.19, and 0.17 birds/km^2 for the South, North, and Smoky sites, respectively.

METHODS

Field Methods

Prairie-chickens were captured at lek sites during the spring with walk-in traps and drop-nets (Silvy et al. 1990, Schroeder and Braun 1991). Captured birds were sexed by plumage characteristics (Henderson et al. 1967). We determined age-class as yearling or adult from the shape, coloration, and wear of the outermost two primaries (numbers 9 and 10; Schroeder and Robb 1993). Morphometrics of adults, including total mass and length of the tarsus–metatarsus, were measured at the time of capture. All birds were individually marked with color leg bands and females were fitted with 11-g necklace-style VHF radio transmitters, equipped with mortality switches and an expected battery life of 12 months (Model RI-2B, Holohil Systems Ltd., Ontario, Canada). Radio-marked females were monitored ≥3 times per week from vehicles during the nesting and brood-rearing period (April–August) and ≥1 time per week during the rest of the year (September–March). Once a female localized in an area for three successive days, we used a portable radio receiver and handheld Yagi antenna to locate the nest. We flushed the female once in early incubation to count the eggs, to determine the stage of incubation, and to record the nest location. Females with nests were monitored daily at a distance ≥100 m by triangulation of the radio signal. Once it was determined that the female was no longer tending the nest, we classified nest fate as successful (≥1 chick produced) or failed.

Body Mass of Females

Reproductive effort of female prairie chickens at the different study sites could be influenced by site differences in food resources if females with heavier body mass were in better nutritional condition and laid larger eggs. Alternatively, site differences in body mass could be a result of seasonal differences in ovarian development among females at capture. We evaluated the first possibility by regressing female mass at capture on length of the tarsus–metatarsus as an index of body size. Residual body mass of females was used as an index of spring body condition before egg-laying. Assessment of ovarian development was difficult because we were unable to determine if females were gravid at capture. We used the interval between the day of capture and the day of nest initiation as a covariate (McNew et al., this volume, chapter 15). Mass of a female grouse increases before the onset of egg-laying (Hannon and Roland 1984), and we expected that females

with shorter intervals between capture and nest initiation were more likely to be gravid. We used analysis of covariance to test whether regional differences in female mass at capture were influenced by the length of time between capture and nest initiation. We tested factorial models with main effects and interaction terms, and all parametric statistics were calculated using procedures of program SAS (ver. 9.1, SAS Institute, Cary, NC).

Clutch Size and Egg Volume

Clutch size was calculated as the maximum number of eggs recorded per clutch once egg-laying was completed and a female had started incubation. We floated all eggs from clutches determined to be in incubation to assess stage of development from egg buoyancy, adjusting for cases where egg-laying rates exceeded one egg per day (McNew et al. 2009, McNew et al., this volume, chapter 15). We measured egg volume only once during incubation to minimize the impacts of nest visits. Egg length (L) and breadth (B) were measured to the nearest 0.1 mm using calipers, and linear measurements were converted to an estimated egg volume (V) with the following equation (Narushin 2005):

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

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

Nest and Brood Survival

Nest survival was the probability of a nest producing ≥1 hatched chick, whereas brood survival was defined as the probability that ≥1 chick survives to fledging at 14 days after hatching. We calculated daily rates of nest and brood survival for each study area with the nest survival model of program MARK (ver. 4.3; White and Burnham 1999, Dinsmore et al. 2002). Multiple model selection and inference was used to evaluate the importance of three factors on daily nest

survival (Burnham and Anderson 1998). The three factors included in the global model for nest survival included nesting attempt (first or renest), female age, and study site. We estimated a corrected probability of nest survival by raising the daily nest survival probabilities to a power equal to the duration of the nest exposure period (37 days; Dinsmore et al., 2002, Sandercock et al. 2005, McNew et al., this volume, chapter 15). This method assumes that daily nest survival is similar across the nest exposure period within a study site. Duration of the nesting cycle was calculated assuming an egg-laying rate of one egg per day and an average incubation period of 25 days (Nooker 2007, McNew et al., this volume, chapter 15). To estimate brood survival prior to fledging, we conducted early-morning flush counts of females attending broods at 14 days post hatch. (Hubbard et al. 1999, Fields et al. 2006). If no chicks were counted, we used subsequent flush counts at 10-day intervals to confirm presence or absence of chicks. We updated 14-day flush counts for 5% of cases from zero to the maximum number of observed chicks at later flush counts. The probability of brood survival to fledging was calculated as the product of the estimates of daily brood survival from the top model for a 14-day period from hatching until fledging. Variances of derived parameters were calculated using the delta method (Powell 2007).

Survival of Females

We estimated monthly survival of female prairie chickens during a two-year period between March 2007 and February 2009 with the nest survival procedure of program MARK. The nest survival model is a general procedure for known-fate data and is useful for estimating survival from "ragged" telemetry data from radio-marked birds (Hartke et al. 2006, Mong and Sandercock 2007). Multiple model selection and inference was used to evaluate the importance several factors on monthly adult survival (Burnham and Anderson 1998), including female age, study area, residual body mass adjusted for tarsus–metatarsus length, and linear and quadratic time trends. We used the most parsimonious model to derive monthly survival probabilities, and then extrapolated annual survival rates at each study area as the product of monthly survival rates during the entire study period. Variances

of derived parameters were calculated using the delta method (Powell 2007).

RESULTS

Body Mass of Females

A total of 203 individual female prairie chickens were captured before egg-laying at our three study areas in Kansas. Reproductive data were available for 159 females. We excluded females for which the capture to clutch initiation interval was less than zero ($n = 8$). Analysis of covariance showed there was no interaction between the effects of study site and the interval between capture and egg-laying ($F_{2,124} = 0.93$, $P = 0.40$). Body mass of female prairie chickens differed significantly among the three study sites ($F_{2,124} = 7.7$, $P < 0.001$), and females were heaviest at the Smoky site (929 $\pm$ 8.8 g), intermediate at the North site (908 $\pm$ 8.7 g), and lightest at the South site (879 $\pm$ 7.9 g; Table 19.1). The interval between capture and egg-laying was unrelated to female mass ($F_{1,124} = 1.7$, $P = 0.20$). Mass did not differ between age-classes ($F_{1,124} = 0.39$, $P = 0.54$), and the interaction between female age and study site was not significant ($F_{1,124} = 0.88$, $P = 0.42$). In addition, the interval between female capture and clutch initiation did not differ among age classes ($F_{1,136} = 1.6$, $P = 0.21$). We found no significant relationship between female mass and tarsus–metatarsus length ($r^2 < 0.01$, df = 1, $P = 0.64$).

Clutch Size and Egg Volume

Analysis of covariance showed there was no interaction between the effects of study area or nesting attempt on clutch size ($F_{2,151} = 0.13$, $P = 0.88$). First nests were consistently larger than renests ($F_{1,151} = 39.1$, $P < 0.001$); the number of eggs per clutch averaged 12.5 to 13.1 eggs for first nesting attempts and 10.2 to 10.9 eggs for renests (Table 19.1). First nests at the Smoky site tended to be larger by about 0.5 eggs per clutch, but overall, clutch size did not differ significantly among study areas ($F_{1,151} = 0.44$, $P = 0.65$). Clutch size did not differ between female age classes (mean $\pm$ SE = 12.7 $\pm$ 0.25 for both groups; $F_{1,141} = 0.98$, $P = 0.32$), and there was no interaction between age-class and study site ($F_{2,141} = 0.28$, $P = 0.75$). Analysis of covariance showed that there was no

interaction between the effects of residual female mass and study area on egg volume ($F_{2,143} = 1.07$, $P = 0.35$). Egg volume differed among the three study areas ($F_{2,142} = 3.2$, $P = 0.04$), with the largest eggs laid at the Smoky site (24.7 $\pm$ 0.2 ml) and the smallest eggs at the South site (23.7 $\pm$ 0.2 ml; Table 19.1). Egg volume did not differ between female age classes ($F_{1,140} = 2.8$, $P = 0.09$), and there was no interaction between age-class and study site ($F_{2,140} = 2.5$, $P = 0.08$). Egg volume was not related to clutch size ($r^2 = 0.01$, $P = 0.20$).

Nest Survival and Brood Survival

During the breeding seasons of 2006–2008, 231 nests of 155 female prairie chickens were located and monitored, of which 44 were successful, for an apparent nest success rate of 19%. Daily nest survival was modeled for a 37-day exposure period during a 103-day nesting season from 23 April to 19 July. The most parsimonious model ($\Delta AIC_c = 0$) included a group effect for study area. Models where nest survival varied among study areas were 9.9 times more likely than models where nest survival was constant ($w_i/w_j = 0.79/0.08$). Variation in survival among study areas accounted for 79% of the relative support of the data. Nest survival was lower at the South site (0.07 $\pm$ 0.02) compared to the North (0.12 $\pm$ 0.03) and Smoky sites (0.16 $\pm$ 0.04; Table 19.1). Overall nest survival for all sites and nesting attempts combined was 0.12 $\pm$ 0.04 SE. Evidence at failed nests indicated that predation was the primary cause of nest mortality, accounting for 94% of all losses.

Forty-three broods were monitored from hatch until fledging at 14 days of age. Daily brood survival during this period was modeled for a 69-day brood-rearing period from 17 May to 24 July. A model that contained an effect of study area was considered parsimonious ($\Delta AIC_c = 0.37$). Models where brood survival varied among study areas had 44% of the relative support. Site differences in brood survival were similar to patterns of nest survival: Survival of broods was highest at the Smoky site (0.45 $\pm$ 0.11), intermediate at the North site (0.32 $\pm$ 0.12), and lowest at the South site (0.24 $\pm$ 0.10; Table 19.1). Overall, the model-averaged estimate of brood survival until fledging across all study areas was 0.35 $\pm$ 0.07.

TABLE 19.1

Mean estimates ($\pm$ SE) for body mass and demographic traits of female Greater Prairie-Chickens breeding at three study areas in eastern Kansas, 2006–2008.

Parameter	South	n	North	n	Smoky	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	$\Delta AIC_c = 0.0$, $w_i/w_j = 7.3$
Brood survival	0.29 (0.09)	15	0.38 (0.09)	12	0.48 (0.12)	16	$\Delta AIC_c = 0.37$, $w_i/w_j = 1.2$
Annual survival of females	0.68 (0.01)	55	0.47 (0.002)	84	0.32 (0.001)	69	$\Delta AIC_c = 0.0$, $w_i/w_j = 99.0$

[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.

Female Annual Survival

Monthly survival probabilities were estimated for 203 females. Model selection based on AIC$_c$ indicated that variation in survival among study sites was strongly supported by the data, accounting for more than 99% of the relative support. Estimates of annual survival extrapolated from monthly rates were greater at the South site (0.68 $\pm$ 0.01) than at the North (0.47 $\pm$ 0.002) and Smoky sites (0.32 $\pm$ 0.001; Table 19.1). Overall annual survival of females during the 12-month period from March to February for all sites pooled was 0.48 ($\pm$0.001).

DISCUSSION

Female Greater Prairie-Chickens breeding at three sites across a gradient of human landscape alteration and use in the Flint Hills and Smoky Hills of Kansas exhibited variation in a suite of eight life-history traits. Females breeding at a study site consisting of large, contiguous blocks of heavily grazed native prairie (South) had the lightest body mass, laid the smallest eggs, and had the lowest clutch volume. Nest and brood survival were low but annual survival was high for prairie chickens breeding in large tracts of heavily grazed and intensively burned prairie. In contrast, females breeding at a highly fragmented, moderately grazed, and infrequently burned site (Smoky) had the heaviest body mass, laid the largest eggs, and had the greatest clutch volume. The Smoky site had the highest rates of nest and brood survival, although our estimates were depressed compared to values compiled for other populations (Peterson and Silvy 1996). In fact, our estimates of annual survival for females at the fragmented Smoky site are among the lowest values ever reported for a field study of prairie chickens. The study site in the northern Flint Hills (North) had intermediate amounts of habitat fragmentation and grazing intensity, and the vital rates of female prairie chickens were intermediate as well. We thus evaluate the potential roles of phenotypic plasticity and evolutionary processes as potential explanations for the results of our demographic analyses.

Trade-offs between realized fecundity and annual survival are often interpreted as resulting from evolutionary processes, but trade-offs can also be produced by phenotypic plasticity and resource limitations (Ricklefs 2000). For example, site differences in female mass in our study could

have been an artifact of differences in date of capture and the degree of gravidity among females before egg-laying. Timing of lek attendance did not differ among the three study areas, but clutch initiation was delayed at the South site, and females at Smoky could have been closer to egg-laying at capture (McNew et al., this volume, chapter 15). Alternatively, variation in female mass could have been the result of site differences in female age structure provided there are differences in mass between yearling and adult females. We reject differences in seasonal phenology as an explanation for variation in female mass at capture, because body mass was not related to the interval between capture and date of nest initiation, and reproductive effort still differed among areas after adjustment for the covariate. Likewise, we reject the latter explanation because the age structure of captured females was similar among sites (~50% yearlings: 50% adults) and female mass did not differ between the age-classes.

Phenotypic plasticity (i.e., the ability of females to alter their reproductive effort based on body condition) could also be relevant if site differences in body mass, clutch size, and egg volume were due to regional differences in food availability that impacted the body condition of egg-laying females. Females had the highest body mass and laid the largest clutches and eggs at the Smoky site, a site fragmented by agricultural development. Cultivated agricultural fields comprised a higher proportion of the landscape at the Smoky site, and prairie chickens will utilize grain sorghum and other crops during winter and early spring (Robel et al. 1970). Two lines of evidence suggest that body condition cannot explain regional variation in reproductive effort of prairie chickens in Kansas. First, residual female mass did not explain variation in egg volume among our three study areas. Food supplementation usually has little impact on egg size of birds but can have larger effects on timing of laying and clutch size (Christians 2002). Estimates of heritability for egg size are often high in birds, suggesting that egg size may be under selective pressures unrelated to the nutritional status of laying females. Second, egg volume of prairie chickens was not related to clutch size. Life-history theory predicts a negative relationship between egg size and clutch size if female resources must be partitioned (Roff 1992), but a positive association would be expected if both traits are impacted by nutritional condition, which we did not observe.

Lower reproductive effort among prairie chickens breeding in heavily grazed contiguous grasslands and higher reproductive effort among prairie chickens in moderately grazed and fragmented grasslands was consistent with life-history theory, which predicts that high nest predation and high adult survival should select for reduced reproductive effort (Roff 1992). Mortality of female prairie chickens was almost entirely the result of predation (90%; L. B. McNew, unpubl. data). Thus, the most important environmental factor leading to divergence in the life-history traits of prairie chickens appears to be the impacts of predators on the survival of adults and nests. We lacked estimates of predator abundance for our three study areas, but fragmentation by agricultural development and road density were ranked Smoky > North > South. Known predators of prairie chickens, such as coyotes (*Canis latrans*), use edge habitats and roads for travel and foraging (Kuehl and Clark 2002, Tigas et al. 2002). Higher-quality nesting and brood-rearing habitat as a result of greater residual cover due to infrequent burning and lower cattle grazing intensity (McNew et al., this volume, chapter 15) could explain greater reproductive success at the Smoky site. Thus, anthropogenic changes in land use and habitat fragmentation may have led to differential rates of exposure to predators. Limited data from prior to large-scale implementation of IESB suggest that nest success of prairie chickens in the Flint Hills was similar (35%) to our estimates from the Smoky Hills (Robel 1970). Therefore, it appears that the direct effects of human activities on grassland ecosystems and the indirect impacts of habitat modification upon predator–prey interactions have influenced the selection of life-history traits of Greater Prairie-Chickens in Kansas over a relatively short time period. Notwithstanding, our results should be viewed in the context of a relatively short-term field study.

There is mounting evidence that human activities have led to ecologically significant evolutionary change in a variety of taxa, and at a range of temporal and spatial scales, contributing to growing interest in the study of contemporary evolution (Carroll et al. 2007, Smith and Bernatchez 2008). Relatively few studies have evaluated the impacts of habitat loss and degradation on the life-history evolution of terrestrial vertebrates. Cutting of grasslands for hay production destroys nests of grassland songbirds, including Savannah Sparrows (*Passerculus sandwichensis*) breeding in dairy pastures in Vermont. Perlut et al. (2008) showed that timing of hay cutting altered mating strategies and the occurrence of extra-pair copulations, as well as the strength of selection on morphological traits. Fencing of pastures for livestock is a landscape modification that poses a risk of collision mortality for female Lesser Prairie-Chickens (Wolfe et al. 2007), and Patten et al. (2005) presented evidence that female prairie chickens subject to higher fence collision mortality laid larger clutches and had a greater probability of renesting than birds at less heavily fenced sites. Our study extends these previous results by showing that landscape modification by humans may lead to differential rates of predation that affect the life-history traits of Greater Prairie-Chickens. Mammalian predators play an important role in structuring terrestrial ecosystems (Pace et al. 1999), but previous studies investigating trophic dynamics have primarily focused on the ecological consequences of the removal of top predators and mesopredator release (Elmhagen and Rushton 2007, Berger et al. 2008). Changes in predator abundance and diversity can also drive evolutionary change in the life-history strategies of lower trophic levels. For example, predators can determine the life-history evolution of guppies (*Poecilia reticulata*) in captivity and natural environments (Reznick et al. 2008). Selective removal of top predators is one way that humans influence life-history evolution, but our results suggest that indirect effects of landscape modification on predation risk can also be important.

Our analysis is one of the first studies to assess the influence of human landscape alteration on the life-history evolution of grouse, and our work could be extended in two ways. First, we observed the impacts of predation on the demographic parameters of prairie chickens but were unable to determine whether variation in predation rates was due to a numerical or a functional response. We lacked estimates of predator abundance, and the identity of major predators was surmised by inspecting the remains of depredated nests and carcasses. Our analyses would be informed by a better understanding of predator abundance and activity in relation to land use and landcover changes. Second, our analyses were based on retrospective comparisons of demographic data for prairie chickens at three study sites over a short time, and life-history traits could have covaried with an environmental factor that we

failed to consider (Ricklefs 2000). Experimental protocols are a stronger approach to testing for local adaptation but would require raising birds in a common environment or reciprocal transplants among different populations (James 1983, Rhymer 1992, Bears et al. 2008). Experimental tests will be logistically difficult for prairie chickens because of their large home range requirements, vagility, and conservation status. Wildlife management activities are rarely considered from an evolutionary perspective but could have potential for analyses of contemporary life-history evolution in prairie chickens. For example, comparisons of performance between wild prairie chickens and pen-reared Attwater's Prairie-Chickens (*T.c. attwateri*) might yield insights into the selection conditions of captive-rearing environments (Peterson and Silvy 1996, Hess et al. 2005). Finally, ongoing translocations of prairie chickens from Kansas to relict populations in Illinois and Missouri (Westemeier et al. 1998, J. C. Pitman, pers. comm.) will provide future opportunities for investigating adaptation in wild populations in new environments.

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