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Habitat fragmentation, rapid evolution and population persistence

Michael A. Patten,[1,2]* Donald H. Wolfe,[1] Eyal Shochat[1]
and Steve K. Sherrod[1]

[1]*Sutton Avian Research Center, University of Oklahoma, Box 2007, Bartlesville, OK 74005 and*
[2]*Department of Zoology, University of Oklahoma, Norman, OK 73019, USA*

ABSTRACT

Associations between extinction and habitat fragmentation have been modelled and described, but we document the first clear mechanistic link between habitat fragmentation and population persistence, demonstrating that a rapid evolutionary response to fragmentation can yield conditions wherein some populations are more vulnerable to extinction. Historical differences in the partitioning and tenure of land in southwestern North America has resulted in vast differences in parcel sizes. Smaller parcels at the eastern edge (western Oklahoma) of the shortgrass prairie are bounded by far more fence and traversed by far more roads and power lines than are larger parcels at the western edge (eastern New Mexico). The increased extent of fencing, roads and power lines is associated with higher mortality of female, but not male, lesser prairie-chickens (*Tympanuchus pallidicinctus*), a rare species endemic to the south-central United States. Differences in mortality rates appear to have selected for differences in life-history strategies: relative to females in New Mexico, female prairie-chickens in Oklahoma lay larger clutches and nest fewer years but make more attempts within a year. The results of this trade-off have left Oklahoma birds far more susceptible to year-to-year environmental perturbations, explaining that population's rapid decline relative to the more stable populations in New Mexico.

Keywords: fragmentation, lesser prairie-chicken, life-history evolution, trade-offs, *Tympanuchus pallidicinctus*.

INTRODUCTION

Habitat fragmentation has a negative impact on population persistence, both immediately and over time (Soulé, 1986; Noss and Copperrider, 1994; Tilman *et al.*, 1994). Persistence generally is thought to be mediated through some form of demographic stochasticity (Simberloff, 1994), although many models neglect to identify a mechanism (Tilman *et al.*, 1994; Pimm and Askins, 1995;

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* Address all correspondence to Michael A. Patten, Sutton Avian Research Center, University of Oklahoma, PO Box 2007, Bartlesville, OK 74005, USA. e-mail: mpatten@ou.edu

Hanski and Gilpin, 1999; Hill and Caswell, 1999). Increased fragmentation increases habitat isolation (Andren, 1994) and may therefore alter population response to habitat change (Segelbacher *et al.*, 2003). In light of extensive and on-going anthropogenic alteration of the environment – ranging from global warming to habitat fragmentation and loss (Soulé, 1986; Noss and Copperrider, 1994) – understanding how fragmentation affects natural populations is vital to conservation efforts, as evolution can occur in a geological instant in response to human-induced change (Rice and Emery, 2003; Stockwell and Ashley, 2004).

We detail a mechanistic, evolutionary explanation for the negative effects of habitat fragmentation in a comparative study of two populations of the lesser prairie-chicken (*Tympanuchus pallidicinctus*), a medium-sized, non-migratory grouse endemic to mixed- and shortgrass prairies of the south-central United States. Both the species' population size and range have shrunk by more than 90% in the past 100 years (Giesen, 1998; Woodward *et al.*, 2001). The decline has been especially sharp in western Oklahoma and the panhandle of Texas. The contiguous population stretching across the panhandle from Oklahoma to eastern New Mexico is no more – the endpoints are now separated by at least tens and often hundreds of kilometres (Fig. 1), many intervening subpopulations having disappeared only since the early 1960s (Sullivan *et al.*, 2000).

Five years (1999–2003) of monitoring lesser prairie-chicken nests in New Mexico and Oklahoma revealed a sharp difference in nesting strategies between these populations: females in the latter are over five times more likely to re-nest within a season. Moreover, long-term surveys suggest that the size of the New Mexico population, although decreasing, is more stable than that of the Oklahoma population. These observations led to a four-pronged investigation: (1) Do other aspects of reproductive effort differ between the study areas? (2) Does survivorship differ between these areas in a manner theoretically associated with differences in reproductive effort? (3) Is there a demonstrable difference in anthropogenic habitat alteration that might explain observed differences in life-history traits? (4) Can observed differences in life history account for apparent differences in population persistence?

METHODS

Study sites and climate

Our study sites were on either side of the Texas (USA) panhandle, in eastern Roosevelt County, New Mexico, and in southern Harper, northern Ellis and easternmost Beaver Counties, Oklahoma (Fig. 1). The sites lay in the shortgrass prairie biome, which supports sand shinnery vegetation dominated by perennial grasses and by shrubs such as *Quercus havardii*, *Artemisia filifolia*, *Gutierrezia sarothrae* and *Prunus* spp.

We compiled 1971–2000 data from weather stations nearest our field sites: Portales, New Mexico (data from the Western Regional Climate Center, Desert Research Institute, Reno, Nevada), and Laverne, Oklahoma (data from the Southern Regional Climate Center, Louisiana State University, Baton Rouge). Monthly mean temperatures are similar between sites, reaching an apex in July (25.4°C in New Mexico, 26.8°C in Oklahoma) and a nadir in January (3.7°C in New Mexico, 0.1°C in Oklahoma). Mean annual precipitation is 44.0 ± 13.2 cm (17.3 ± 5.2 inches; coefficient of variation = 0.31) in New Mexico and 56.1 ± 14.8 cm (22.1 ± 5.8 inches; coefficient of variation = 0.25) in Oklahoma. Rainfall in late spring and summer accounts for over half of the annual total for each site (New

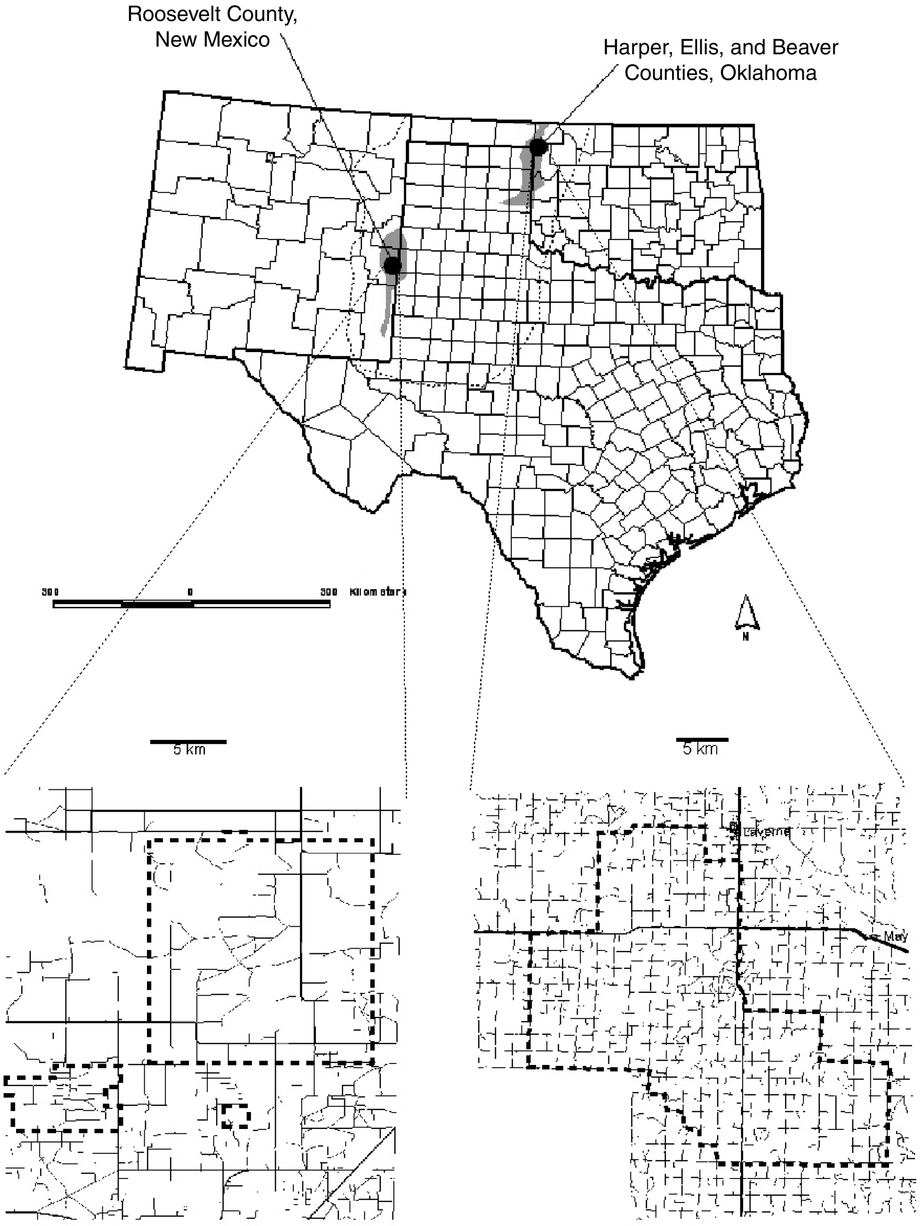

Fig. 1. The former (dotted line) and current (shaded) distribution of the lesser prairie-chicken in New Mexico, Texas and Oklahoma. The expanded views of our New Mexico and Oklahoma study sites (dashed lines) show the much greater extent of roads (solid lines) in the latter. The extent of fencing and power lines is positively correlated with the extent of roads (Spellerberg, 1998). Our study areas contained land tenure patterns typical of each region.

Mexico: 56.2% June–September; Oklahoma: 50.5% May–August). Neither site receives much of its rain in winter, that is November–February (New Mexico: 14.2%; Oklahoma: 16.3%).

Radiotracking and survivorship

From April 1999 to September 2003, we tracked 160 radio-tagged females, 98 in New Mexico and 62 in Oklahoma, each affixed with a loop-antenna transmitter with a battery life of approximately 1.5–2 years. Birds generally were tagged on spring leks ($n = 11$ in each state) using a modified walk-in trap (Schroeder and Braun, 1991). We monitored activities of all radio-tagged females year round but particularly during the breeding season (May–July). We located 160 nests (92 in New Mexico, 68 in Oklahoma) from 90 different females (58 in New Mexico, 32 in Oklahoma). We estimated mean reproductive value broadly as $\Sigma m_x S_x$, where m_x is birth rate and S_x survivorship at age x.

We calculated the number of days each radio-tagged male (188 in New Mexico, 191 in Oklahoma) and female (93 in New Mexico, 62 in Oklahoma) survived since being radio-tagged. Because we tracked birds continuously after capture, we did not require capture–mark–recapture methods to estimate survival. Instead, we constructed survival curves using a product-limit (Kaplan-Meier) estimator (see Pollock *et al.*, 1989) and compared these curves using −2 log likelihood log-rank χ^2 tests. Birds were captured at random, so each individual 'entered' the study at an arbitrary point with respect to age.

Mortality

We determined cause of death using standard protocols (Dumke and Pils, 1973), although an exact determination can be difficult because both raptors and mammals scavenge dead prairie-chickens. We recorded the distance from the nearest fence, road and power line, and documented tracks, scat, hair and other clues. After examination in the field, we photographed and salvaged all carcasses, the latter under permits 3025 with the State of New Mexico, 3389 with the State of Oklahoma, SPR-0500-100 with the State of Texas, and 21947-H with the United States Fish and Wildlife Service.

For both males and females, we constructed non-parametric regression equations (proc loess, SAS Statistical Software, version 8e, SAS Institute, Cary, NC) with mortality as the response variable and predation, collisions, or both as the predictors. We used the modified Akaike Information Criterion (AIC_c) to compare model fit. We estimated relative fitness on the basis of proportion of known mortalities.

Population model

We estimated the probability of population persistence using a simple model:

$$N_{i+1} = (N_i + f)lp$$

where

$$f = \tfrac{1}{2}(mnsN_i)e_i$$

and N_i is the population size in year i, m is the mean number of fledglings per nest, l is the probability of survivorship per year, n is the number of nesting attempts per year, s is the proportion of successful nests, p is the proportion of females surviving to N_{i+1} that nest that year, and e_i is the environmental stochasticity (a random variable, varying between 0 and 1, where 0 represents the 'worst' possible year and 1 the 'best' year). Assumptions were of a 1 : 1 sex ratio, constant post-juvenile mortality and reproductive effort across years and, in a given year, environmental stochasticity had the same effect on each site, a plausible assumption given the similar climate. Parameters were estimated from our field data. This model is far from comprehensive; we used it only as a means of demonstrating that environmental stochasticity could lead to extinction given certain combinations of life-history traits.

RESULTS

Reproductive effort

Neither mean lifetime nesting effort per female lesser prairie-chicken (New Mexico, 2.20 ± 0.09; Oklahoma, 2.37 ± 0.14; mean ± standard error) nor their mean reproductive values (New Mexico, 5.81; Oklahoma, 5.71) differed between states. But how nesting effort was partitioned differed substantially: females in the Oklahoma population nested fewer years but more often within each year (Table 1). Moreover, reproductive output – both clutch size and fledgling production – was higher for females in Oklahoma (Table 2) despite a nearly identical proportion of successful nests between the two populations (0.42 [39 of 92] in New Mexico, 0.40 [27 of 68] in Oklahoma). The difference in reproductive effort was not associated with mean climate conditions (which are broadly similar; see Methods section), the length or timing of the breeding season, or female condition. The median nest date was 12 May in New Mexico (range 29 April–11 June, mode 3 May; $n = 88$) and 22 May in Oklahoma (range 30 April–5 July, mode 6 May; $n = 68$). The distributions of nest dates were slightly right skewed, but expressed as means ± standard deviation, ~72% of nests were initiated 13 May ± 10 days in New Mexico and 23 May ± 17 days in Oklahoma. Weights (our surrogate of condition) of females caught in spring (March–May) did not differ between sites (New Mexico: 725.6 ± 57.3 g, range 600–850 g, $n = 27$; Oklahoma:

Table 1. Comparisons of nesting effort between New Mexico ($n = 63$ females) and Oklahoma ($n = 42$) populations of the lesser prairie-chicken, 2000–2003

Population	Years nesting[a]			Attempts per year (mean ± SE)	Proportion re-nesting in same year
	1	2	3		
New Mexico	1	17	2	1.07 ± 0.04	0.15
Oklahoma	9	10	0	1.55 ± 0.11	0.79

Note: The relative frequencies of nesting for multiple years differ significantly between the states ($G_2 = 11.94$, $P < 0.005$). The differences lie in the tendency of females in Oklahoma to re-nest within a given year ($t_{37} = 4.18$, $P < 0.001$). Differences in the proportion of females re-nesting within the same year are particularly striking ($G_1 = 121.42$, $P < 0.0001$).

[a] To avoid biasing the results towards birds first nesting in 2003 (i.e. we do not know if they nested in 2004), data for years nesting include only those females for which at least two nests were located (20 in New Mexico, 19 in Oklahoma). Inclusion of all birds that first nested 2000–2002 raises totals for the first column to 23 for New Mexico (54.8% of birds nested in only one year) and 24 for Oklahoma (70.6% nested once).

Table 2. Comparisons of reproductive output between New Mexico and Oklahoma populations of the lesser prairie-chicken

	Clutch size (mean ± SE)			Fledglings/female (mean ± SE)	
Population	Overall*	Adult	Yearling	All females	Successful only
New Mexico	8.73 ± 0.26	9.29 ± 0.33	7.67 ± 0.39	3.66 ± 0.57	7.07 ± 0.63
Oklahoma	10.81 ± 0.42	10.83 ± 0.52	10.88 ± 0.88	4.50 ± 1.05	11.08 ± 0.98

Note: Data were averaged by female (58 in New Mexico, 32 in Oklahoma) before averaging by population. As predicted by the theory of life-history evolution, mean clutch size was higher in Oklahoma ($t_{88} = 4.33$, $P < 0.0001$), where female mortality is higher. Clutch size depended on the female's age in New Mexico ($t_{50} = 3.14$, $P < 0.01$) but not in Oklahoma ($t_{25} = 0.01$, $P > 0.90$). The mean number of fledglings per female was one chick higher in Oklahoma, but the difference was not significant ($t_{88} = 0.77$, $P > 0.25$). However, the number of fledglings per female for successful nests only was four chicks higher in Oklahoma ($t_{41} = 3.48$, $P < 0.01$).

[a] Includes birds of unknown age. Excluding clutches from second nests raised the Oklahoma mean to 11.36 ± 0.39 but left the New Mexico mean unchanged. Excluding all later clutches (after 15 May) yielded New Mexico 8.82 ± 0.33, Oklahoma 12.13 ± 0.35.

720.8 ± 52.2 g, range 595–830 g, $n = 37$). Although we sampled multiple leks, 11 in each state, because of spatial autocorrelation we did not treat individual leks as replicates. Our results would not have changed if we had, however, as reproductive output is relatively high across Oklahoma leks and low across New Mexico leks (the same holds for mortality rates and causes).

Survivorship and mortality

Given our observations of (a) increased nesting effort within a year but decreased effort across years and (b) increased reproductive output per nest, trade-offs in life-history traits (Lande, 1982; Partridge and Harvey, 1988; Partridge and Sibly, 1991; Zera and Harshman, 2001) implied that female mortality is significantly higher in Oklahoma. For example, our findings are consistent with research on other species of North American grouse, in which clutch size varies in direct proportion to mortality, generally being 5–8 eggs if annual mortality rates are below 50% but 9–13 eggs if annual rates exceed 55% (Bergerud, 1988). Our findings (Table 2) are also consistent with those of prior studies in that yearling grouse laid fewer eggs only in populations with low mortality rates (Bergerud, 1988).

We compared survivorship of birds between the populations, confirming that female but not male mortality was significantly higher in Oklahoma (Fig. 2). Analysis of lesser prairie-chicken carcasses recovered on our field sites showed that causes of mortality differed markedly between the two states (Fig. 3). In particular, the percentage of mortalities resulting from collisions with fences, power lines or vehicles was three times higher in Oklahoma (42.4%) than in New Mexico (14.3%). The timing of mortality differed between the sexes: 42.9% of males died from March to May, coinciding with peak lekking activity (Giesen, 1998), whereas 51.9% of females died in May and June, coinciding with their movement between leks and the period in which they search for suitable nest sites (Giesen, 1998).

Males are more vulnerable to predation when exposed during lek displays than at other times of the year. Consistent with this observation, male mortality was associated chiefly with predation (Table 3, Fig. 4). Excluding mortalities resulting from collisions showed that mortality resulting from predation was effectively identical between the populations

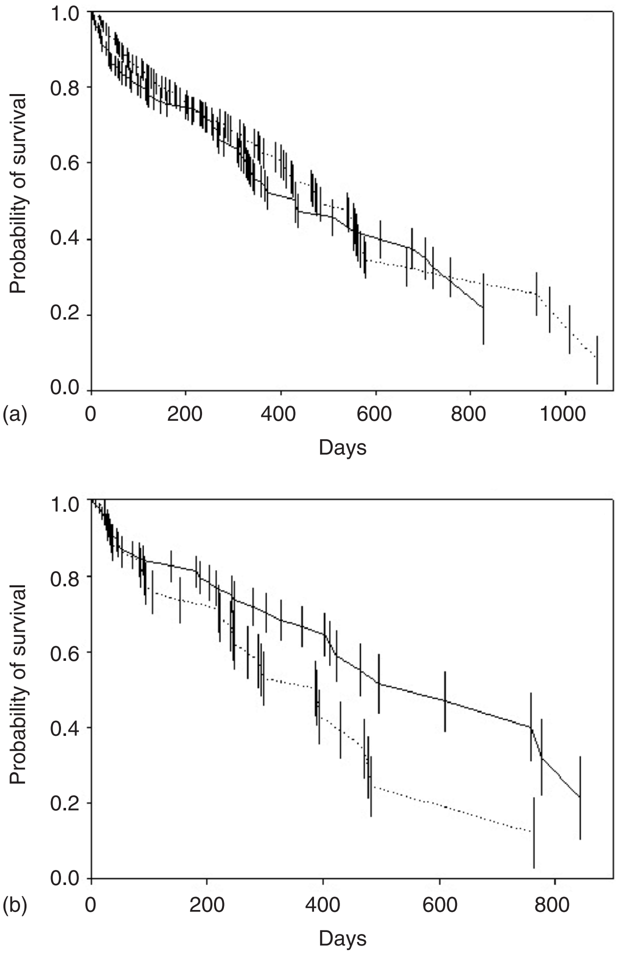

Fig. 2. Survivorship of (a) male and (b) female lesser prairie-chickens in New Mexico (solid line) and Oklahoma (dotted line). Male survivorship does not differ between the populations ($\chi^2 = 0.30$, d.f. = 1, $P > 0.50$), but female survivorship is significantly lower in the Oklahoma population ($\chi^2 = 4.38$, d.f. = 1, $P < 0.04$).

(New Mexico: raptor 57.1%, mammal 42.9%; Oklahoma: raptor 56.9%, mammal 43.1%). A regression model of male mortality with predation as the only predictor fit much better ($AIC_c = 1.66$) than a model including collisions ($AIC_c = 2.21$) or with collisions only ($AIC_c = 4.37$).

Females also visit leks, but do so less frequently and less conspicuously. Unlike males, females typically visit more than one lek during spring (Schroeder, 1991; Sutton Avian Research Center, unpublished data), sometimes as many as five, and females often nest far from the lek where mating took place (Schroeder, 1991; Giesen, 1998). In our tracking studies, across their lifetimes females ($n = 152$) moved nearly twice as far as males ($n = 376$) on average (1119.9 ± 1029.7 m *vs* 687.0 ± 571.8 m; Satterthwaite $t_{190} = 4.89$, $P < 0.0001$). Increased movement of the females renders them less susceptible to predation but more susceptible to collisions with fences, power lines or vehicles (Table 3, Fig. 4), a pattern similar to other species of grouse

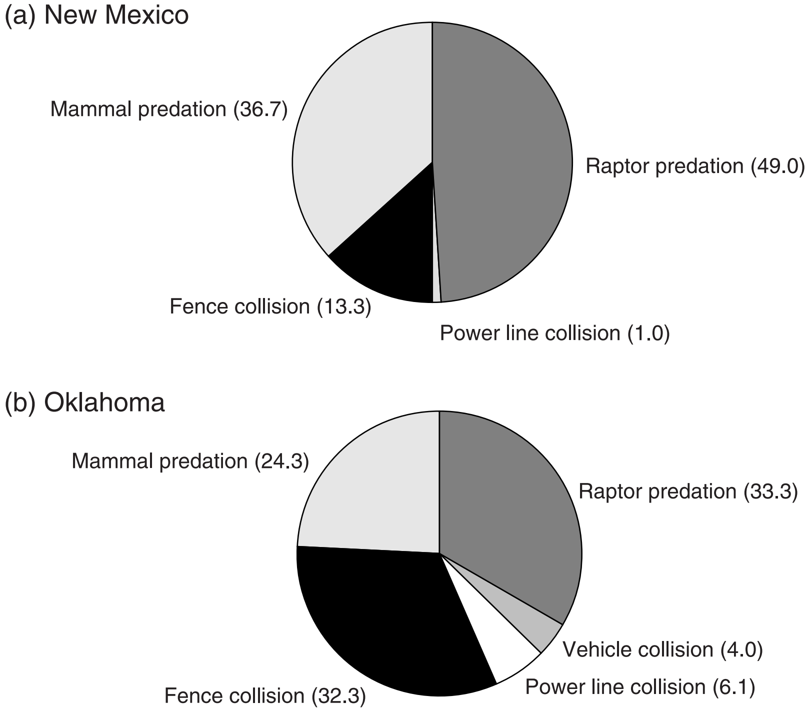

Fig. 3. Causes of mortality in (a) New Mexico ($n = 98$ carcasses) and (b) Oklahoma ($n = 100$ carcasses) populations of the lesser prairie-chicken. More than eight of every ten (85.7%) deaths in New Mexico is the result of avian or mammalian predation, whereas more than four of every ten (42.4%) in Oklahoma is the result of a collision with a fence, power line or vehicle. The proportion of collisions is thus significantly higher in Oklahoma ($G_1 = 20.0$, $P < 0.001$).

Table 3. Correlation (Kendall's τ) matrix of mortality causes of male and female lesser prairie-chicken

Sex	Female	Predation	Collision
Male	0.30 (>0.20)	**0.82** (<0.001)	0.28 (>0.20)
Female		0.29 (>0.20)	**0.48** (<0.05)
Predation			0.26 (>0.25)

Note: The probability of rejecting the null hypothesis of no correlation appears in parentheses below the correlation coefficients. Data are from 254 mortalities (175 male, 79 female) for which cause was determined. Male mortality was associated with predation, whereas female mortality was associated with collisions.

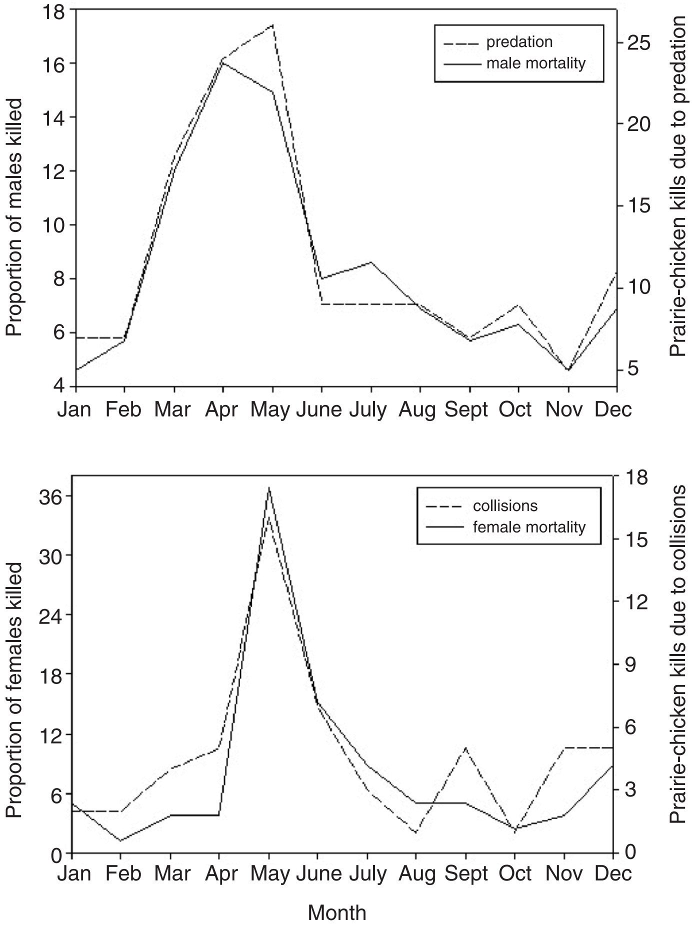

Fig. 4. Annual trends in mortality of male and female lesser prairie-chickens. The sexes differ in the principal causes of mortality: males are depredated far more often than females, but females collide with objects far more often than males. Thus, most mortality from predation is associated with lekking males (March to mid-June), whereas most mortality from collisions is associated with nesting females (April through June).

such as the capercaillie (*Tetrao urogallus*), in which females accounted for 11 of 12 definite fence collisions over a 3-year period (Moss *et al.*, 2000). A regression model of female mortality with collisions as the only predictor fit slightly better ($\mathrm{AIC_c} = 4.34$) than a model including predation ($\mathrm{AIC_c} = 4.47$) but clearly better than one with predation only ($\mathrm{AIC_c} = 5.91$).

Landscape history

Our comparison of recent (1964–1997) land tenure in rural New Mexico and Oklahoma supports this conclusion. Parcel size of farms and ranches is nearly tenfold larger in the former state, averaging 1300 ha compared with 180 ha in the latter (National Agricultural Statistics Service, 1997). Our New Mexico study site is made up of large pastures, many approaching 8 km^2 (770 ha), with some infusion of irrigated crop circles (Fig. 1). Our Oklahoma study site consists of square mile (2.6 km^2) sections often fenced in ¼-section (65 ha) pastures or row crops (Fig. 1). As a result of differences in land partitioning, the Oklahoma site is considerably more fragmented and contains 2–3 times the extent of fences, roads and power lines: a sample of eight 10-km^2 plots selected randomly in each study area had 8.0 ± 2.3 km of road in New Mexico but 14.5 ± 1.7 km of road in Oklahoma ($F_{1,14} = 9.16$, $P < 0.01$). Roads, fences and power lines are strongly associated with each other (Spellerberg, 1998), as land owners frequently fence their property, power lines are virtually always followed by an access road, and right-of-way roads tend to cut between property boundaries.

Despite New Mexico (1912) and Oklahoma (1907) being among the last US territories to be granted statehood, these differences in land tenure have historical bases. New Mexico has a long history of Spanish settlement, including the bestowment of large land grants – many over 5000 ha – from the late 1600s to the mid-1800s (Cline, 1964). In the eastern part of the state, where the lesser prairie-chicken ranges, a sparse human population and arid conditions have favoured low settlement density and large property size. By contrast, Oklahoma has a long history of Native American settlement and relocation. The Sooner and Boomer land rushes from 1889 to 1904 opened the western part of the territory, where the lesser prairie-chicken ranges, to settlers, each of whom was granted a small (~64 ha) parcel (Lynn-Sherrow, 1996). Economic hardships forced the consolidation of various farms and ranches, such that by 1920 the average parcel size had doubled (Lynn-Sherrow, 1996), though it remained far below the average parcel size in New Mexico.

DISCUSSION

Our data show consistent differences in clutch size, fledglings produced and nesting effort between populations of the lesser prairie-chicken in Oklahoma and New Mexico. In each case, reproductive output and effort is higher for females in Oklahoma. Our data also show consistent differences in female survivorship between the populations, with shorter life spans in Oklahoma, and consistent differences in mortality causes for females and males, the former dying chiefly from collisions with man-made objects. Differences in the principal causes of mortality imply differences in the environment experienced by each population of the lesser prairie-chicken. Because male survivorship does not differ between populations, and because the incidence of raptor and mammal predation is virtually identical, we suggest that males experience these environments similarly. Females, on the other hand, collide far more in Oklahoma and have a lower probability of survival in that population, implying that the opportunity for collisions is higher there.

We interpret our results – on reproductive effort, survivorship and land tenure – in terms of established principles of life-history evolution, the underpinnings of which enjoy some of the strongest empirical and theoretical support in all of the biological sciences (Stearns, 1992; Roff, 2002). A well-established result, at least for birds, is the inverse relationship between fecundity and survivorship, traits that typically cannot be maximized simultaneously and typically are associated with environmental variation (Lande, 1982; Ricklefs, 1983; Partridge and Harvey, 1988; Partridge and Sibly, 1991; Zera and Harshman, 2001). Life-history traits are heritable and may be subject to strong selection (Price and Schluter, 1991; Réale and Festa-Bianchet, 2000). In our case, the daily probability of a female lesser prairie-chicken surviving a collision is substantially higher in New Mexico (0.9995) than in Oklahoma (0.9980). As a result, over their lifetimes females in Oklahoma (0.314) are three times more likely to die from a collision than are females in New Mexico (0.116), thus providing a strong selection differential. Nevertheless, we cannot eliminate the possibility that differences in reproductive output may be the result of phenotypic plasticity, but if they are then we expect a direct relationship between output and environmental variation. A plot of clutch size, a good indicator of output, and precipitation, a good indicator of food availability and habitat quality, shows no relationship between these variables (Fig. 5). Regardless of rainfall amounts, clutch size is fairly consistent within a site and is always higher in Oklahoma.

Even though traits associated with a species' life history can evolve rapidly if selection pressure is strong (Gibbs and Grant, 1987; Smith *et al.*, 1995; Reznick *et al.*, 1997; Patten and Campbell, 1998), as yet there is little evidence of natural selection of life history as a result of differing levels of anthropogenic habitat fragmentation. We suggest that increased fragmentation, here defined as any discontinuity in habitat (see Franklin *et al.*, 2003), in Oklahoma has increased the mortality rate and selected for increased reproductive effort in female lesser prairie-chickens. The generation time of a prairie-chicken is about 2 years (Bellinger *et al.*, 2003), meaning that the birds have had over 50 generations to respond to environmental differences, more than enough time when considering that changes in life history can be detected in under 20 generations (Reznick *et al.*, 1997) and rapid evolution has been well documented (Rice and Emery, 2003; Stockwell and Ashley, 2004).

We conclude that differences in land tenure have created an environment in Oklahoma in which the peripatetic females are far more susceptible to collisions with fences, power lines and vehicles. The difference is not one of greater fragmentation in the classical sense (i.e. a disruption of suitable habitat by the proliferation of unsuitable habitat), because habitat on either side of a fence or road tends to be the same. Rather, this type of fragmentation is more insidious, as it subdivides suitable habitat in a way that may be imperceptible with remote sensing or a broad view of the landscape. Classical analyses of fragmentation effects may detect associations with declining numbers of lesser prairie-chickens (Woodward *et al.*, 2001;

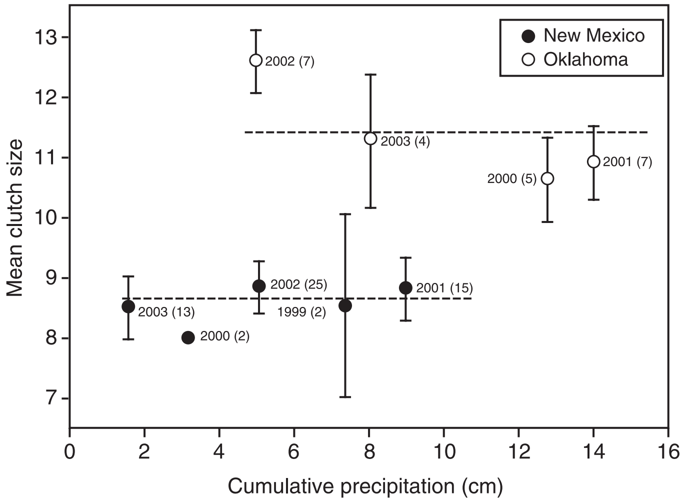

Fig. 5. Mean (±standard error) clutch size of the lesser prairie-chicken in relation to cumulative precipitation, summed for January, February and March, the 3 months before the onset of nesting. Note that rainfall immediately preceding oögensis is a good predictor of clutch size (Patten and Rotenberry, 1999). Sample sizes, with replacement clutches excluded, are shown in parentheses following the year. Dashed lines signify the grand mean at each site.

Fuhlendorf *et al.*, 2002), but they lack a mechanistic link to the declines. Grouse mortality increases as the linear extent of power lines increases (Bevanger, 1995), and grouse appear to be far more susceptible to fence collisions than are other birds. For example, the red grouse (*Lagopus lagopus scoticus*), black grouse (*Tetrao tetrix*) and capercaillie together accounted for >90% of all avian collisions along fences in Scotland (Baines and Summers, 1997; Baines and Andrew, 2003). Changes in land tenure in Texas, where numbers of the lesser prairie-chicken have declined sharply (Giesen, 1998; Sullivan *et al.*, 2000), have led to a steady reduction in mean parcel size since the 1950s (Schmidly, 2002). Oklahoma has mirrored this trend, as the mean farm size has declined from a peak of 260 ha in 1948 (Lynn-Sherrow, 1996) to 180 ha in 1997 (National Agricultural Statistics Service, 1997).

The indirect causal link of change in life history that we postulate is comparable to other examples of evolution in response to anthropogenic alteration of the environment (Hoffmann and Parsons, 1997) – perhaps including reproductive data from a fragmented population of the greater sage-grouse, *Centrocercus urophasianus* (Schroeder, 1997) – but its ramifications for population persistence are of even greater interest. Because female lesser prairie-chickens are tending to concentrate their breeding effort within a single year, the Oklahoma population is more susceptible to annual environmental stochasticity (Leigh, 1981; Lande, 1993; Reed *et al.*, 2003) and therefore has a higher probability of going extinct in the near future (Fig. 6). Not only is the population more susceptible, but the region itself is particularly sensitive to variability (temporal and spatial) in climate and is likely to be negatively affected by global climate change (Legates and DeLiberty, 1996). An explanation has not been forthcoming for the

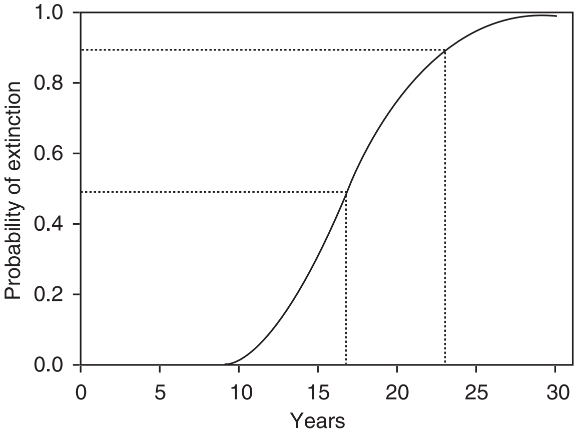

Fig. 6. Probability that the Oklahoma population of the lesser prairie-chicken will become extinct in the next 30 years. Results are from 5000 replicates of a simulation study, based on a simple model of population persistence (see Methods) begun with a population of 1000 females. In as many replicates, the New Mexico population never went extinct over the same time period, and in only 5.5% of simulations was that population below 1000 females by year 30. As a result of population-level differences in female survival and the tendency of females to distribute reproductive effort within years or across years, most variation in population size was the result of year-to-year environmental stochasticity (e_i), here treated as a random probability for year i along a continuum from a very good year (e_i near 1.0) to a very bad year (e_i near 0.0). The average environment needed to achieve population stability ($\hat{e}$) was much higher for Oklahoma ($\hat{e} = 0.7480$) than for New Mexico ($\hat{e} = 0.3765$), meaning the former population could withstand far fewer bad years. Dotted lines mark the points where the probability of extinction is 0.5 (approximately year 17) and 0.9 (approximately year 23).

species' persistent, sharp decline in Oklahoma compared with its much less steep decline in New Mexico (Giesen, 1998; Woodward *et al.*, 2001). Our study linking differences in land tenure to differences in survivorship and, ultimately, to differences in life history predicts a more rapidly declining population in Oklahoma, a prediction consistent with long-term data.

Until now there has been little evidence that habitat fragmentation can affect life-history traits in such a way as to decrease markedly the probability of population persistence. We may not be able to eliminate phenotypic plasticity or non-adaptive geographic variation with a coincidental negative relationship between reproductive output and survivorship, but each of our results is consistent with hypothetico-deductive predictions generated from life-history evolution theory. Considered within this framework, were it not for the striking differences in reproductive effort between the populations, we would not have tested predictions about sex-related differences in mortality or sought to discover the cause for those differences. That predicted differences in mortality exist, are striking enough to create strong selection pressure, and are rooted in historical land use patterns combine to underscore the plausibility of the mechanism.

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