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AGE-SPECIFIC VARIATION IN APPARENT SURVIVAL RATES OF MALE LESSER PRAIRIE-CHICKENS

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Abstract. We used mark-recapture methods to estimate age-specific apparent survival rates for male Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*), a gamebird of conservation concern. A total of 311 male prairie-chickens (135 yearlings, 176 adults) were captured and banded during a 5-year study in southwest Kansas. Time-since-marking models were used to estimate apparent survival after first capture (ϕ^1), apparent survival among returning birds (ϕ^{2+}), and probability of capture (p) for yearling and adult prairie-chickens. Apparent survival is the product of true survival and site fidelity, and our model-averaged estimates of this parameter were ranked: yearlings after first capture ($\hat{\phi}^1_{yr} = 0.60 \pm 0.12$) $>$ adults after first capture ($\hat{\phi}^1_{ad} = 0.44 \pm 0.10$) $>$ returning birds ($\hat{\phi}^{2+} = 0.36 \pm 0.10$). In contrast, movement data showed that site fidelity to communal display sites (or leks) increased with male age; yearlings returned to leks at lower rates (80%, $n = 60$) than adults (92%, $n = 65$). Thus, true survival rates of male Lesser Prairie-Chickens likely decline with increasing age, an unusual pattern found in few species of birds. We hypothesized that declines in survival as males' age may be a feature of promiscuous mating systems where competition for mating opportunities are intense. A review of annual survival rates for holarctic grouse did not support this idea; age-specific declines in male survival were not restricted to lek-mating species, and appear to be a general feature of most grouse populations.

Key words: age-specific demography, grouse, Kansas, mark-recapture, Tetraonidae, Tympanuchus pallidicinctus.

Varición Edad-Específica en las Tasas de Supervivencia Aparente de los Machos en *Tympanuchus pallidicinctus*

Resumen. Empleamos métodos de marcado y recaptura para calcular los porcentajes de supervivencia de machos de la especie *Tympanuchus pallidicinctus*, un ave de caza cuyo estatus de conservación es preocupante. Un total de 311 individuos (135 añales y 176 adultos) fueron capturados y anillados durante 5 ãnos de estudio en el suroeste de Kansas. Para calcular la supervivencia aparente después de la primera captura (ϕ^1), la supervivencia entre las aves que retornan (ϕ^{2+}) y la probabilidad de captura (p) de individuos añales e individuos adultos, se utilizaron modelos del tiempo transcurrido desde el momento de marcado. La supervivencia aparente es el producto de la supervivencia real y la fidelidad al sitio. Nuestros estimados de este paramétro promediados entre modelos fueron: añales después de la primera captura ($\hat{\phi}^1_{yr} = 0.60 \pm 0.12$) $>$ adultos después de la primera captura ($\hat{\phi}^1_{ad} = 0.44 \pm 0.10$) $>$ aves que regresaban ($\hat{\phi}^{2+} = 0.36 \pm 0.10$). En contraste, los datos de movimiento muestran que la fidelidad a los lugares de despliegue comunales (o leks) aumentó con la edad de los machos; los individuos añales retornaron a estos lugares a una tasa (80%, $n = 60$) menor que los adultos (92%, $n = 65$). Así, las tasas de supervivencia verdaderas de *T. pallidicinctus* parecen declinar con el aumento de edad, lo que representa un patrón raro encontrado en pocas especies de aves. Formulamos la hipótesis de que la disminución de la supervivencia conforme los machos envejecen puede ser una característica de los sistemas de apareamiento promiscuo, en los que la competencia por la oportunidad de aparearse es intensa. Una revisión de los porcentajes anuales de supervivencia de urogallos en la región holártica no apoya esta idea; las disminuciones de la supervivencia de los machos con la edad no están limitadas a especies que se aparean en leks, sino que parecen ser comunes a la mayoría de las poblaciones de urogallos.

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INTRODUCTION

Many short-lived species of birds exhibit age-specific variation in demography, with reproductive and survival rates improving with increasing age (Sæther 1990, Martin 1995, Sæther and Bakke 2000). Patterns of age-specific variation in demography may be affected by either natural or sexual selection. For example, high predation on juvenile life-stages should favor reduced reproductive effort, whereas predation of adults favors early maturity and high reproductive effort (Reznick et al. 1990, Martin 2002). Similarly, if mating success is limited to older individuals in one sex but not the other, sexual selection may lead to pronounced differences in the age-specific demographic rates of males and females (McDonald 1993). While it can be challenging to determine the factors that lead to age-specific variation in demography, identifying such patterns is important for the goals of both conservation biology and evolutionary ecology.

Grouse (Phasianidae: Tetraoninae) exhibit a range of mating systems (Johnsgard 1983) and provide an excellent opportunity to investigate the hypothesis that sexual selection affects age-specific survival of males. In socially monogamous grouse species, males defend a territory and a mate, and may participate in parental care. Most males are able to obtain mates and breed as yearlings; a few older males may be facultatively polygynous (Hannon and Martin 1992). In a monogamous mating strategy, little or no age-specific variation in male survival might be expected. In promiscuous breeding species, males do not defend resources required by females or care for young, and compete for mates through display at either dispersed arenas or communal lek sites. If competition for mates at communal display sites entails higher energetic costs or a greater risk of predation, age-specific variation in male survival should be greater among lek-mating species than monogamous species. Mating success is strongly skewed among lek-mating grouse, with relatively few males accounting for most of the copulations (Wiley 1974, Angelstam 1984, Vehrencamp et al. 1989). Mating success often varies with age, and older males tend to be more successful (Robel 1970, Hamerstrom and Hamerstrom 1973, Wiley 1978, Andreev et al. 2001). Because yearling males are less successful at acquiring copulations they may reduce their energetic costs and predation risks by minimizing their attendance and activity rates at lek sites (Robel 1970, Emmons and Braun 1984, Walsh et al. 2004).

The objectives of this study were two-fold. First, we estimated annual survival rates for male Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*), a lek-mating species of grouse. Lesser Prairie-Chickens are a gamebird of conservation concern because their distribution and abundance has declined by >90% over the past century, and this species is currently restricted to remnant mixed-grass and shrub prairies in Colorado, Kansas, New Mexico, Oklahoma, and Texas (Giesen 1998). Better estimates of demographic rates will aid conservation efforts for remaining populations of this candidate species of conservation concern (U.S. Department of Interior, Fish and Wildlife Service 2002). Second, we review age-specific estimates of annual survival for grouse to examine the hypothesis that sexual selection affects age-specific variation in demography.

METHODS

Trapping and monitoring were conducted on two fragmented patches (ca. 5000 ha each) of native sand sagebrush prairie (*Artemisia filifolia*) south of Garden City, Finney County, Kansas. In 1998–2002, we trapped on Area I (37°52′N, 100°59′W) and expanded our study site to include Area II (ca. 15 km east) in 2000–2002 (Hagen 2003). Lesser Prairie-Chickens were captured at all known leks (>3 displaying males, $n = 20$) during spring (March–April) using walk-in funnel traps (Haukos et al. 1990). Traps were rotated among groups of two to three leks every 7–11 days (7.9 ± 1.7), and each rotation was defined as a trap-period. From 1998–1999, two to three leks were trapped simultaneously on Area I per trap-period (3–4 periods per spring), and four to six leks were trapped per trap-period for 3 years following the addition of Area II (Table 1). At first capture, male prairie-chickens were marked with a uniquely-numbered aluminum leg band (provided by the Kansas Department of Wildlife and Parks), and were aged as yearling (ca. 10 months of age) or adult (≥22 months) based on plumage characteristics (Amman 1944, Copelin 1963). Yearlings were identified by pointed and frayed tips of the ninth and tenth primaries, and white spotting within 2.5 cm of the tip of the tenth primary; the absence of these characters indicated the bird was an adult.

SURVIVAL ANALYSES

To estimate apparent survival (ϕ), we applied mark-recapture models for open populations to live encounter data. Apparent survival is the product of two probabilities, true survival (*S*) and site fidelity (*F*). Losses to mortality and permanent emigration cannot be distinguished, thus, we used movements among leks between years to evaluate the possible effects of breeding dispersal on our estimates of apparent survival. To compare lek site-fidelity of yearlings and adults, we examined the frequency and distance of movements among leks for banded prairie-chickens that were recaptured in the year after first capture (Jamison 2000, Hagen 2003). Some males were radio-marked but because of small sample sizes and battery longevity, we were unable to provide annual estimates of age-specific survival using this technique.

We used time-since-marking models (TSM, Cooch and White 2004) that separate apparent survival in the interval after first capture (ϕ^1), from subsequent intervals (ϕ^{2+}). TSM models control for individuals that are captured on only one occasion and never re-encountered. If a sample contains a large number of individuals with this type of capture history, then ϕ^1 is likely to be less than ϕ^{2+}. Estimates of apparent survival for birds based on TSM models are typically ranked: juveniles after first capture < adults after first capture < returning birds (Blake and Loiselle 2002, Cilimburg et al. 2002, Jones et al. 2002, Sandercock 2003). Such patterns can be due to age effects on true survival, or may be explained by heterogeneity of capture, inclusion of transients, or some combination of these factors (Sandercock and Jaramillo 2002).

Mark-recapture analyses were conducted in Program MARK (Cooch and White 2004) following three steps: 1) selection of the global model, 2) goodness-of-fit tests, and 3) fitting and selection of reduced models with fewer parameters. We included age-class at banding (*age*) and time-dependence (*t*) to investigate the effects of age and annual variation on apparent survival (ϕ). We modeled recapture probability (*p*) as a function of time (*t*) and trapping effort (*e*), which reduced the number of parameters needed to explain annual variation in *p*, thus our global model was: ϕ^1_{age*t}, ϕ^{2+}_{t}, p_{age*t}.

A parametric bootstrap goodness-of-fit test was used to test whether mark-recapture data met the assumptions of independence and no heterogeneity. Model fit was calculated as 1–rank n^{-1}, where rank = the rank of the observed deviance of the global model within the bootstrap distribution of expected deviances, and n = 1000 the number of bootstrap replicates (Cooch and White 2004). A variation inflation factor ($\hat{c}$) was then calculated as the observed deviance divided by mean expected deviance from the bootstrap distribution, and was set to one if $\hat{c} < 1$ (Burnham and Anderson 1998).

After examining the fit of the global model, models with fewer parameters were fit to the data. The number of potential models was large and we used a hierarchical procedure to guide model fitting (Lebreton et al. 1992). Our primary interest was ϕ, thus *p* was modeled first as a nuisance parameter. In both ϕ and *p*, we started with factorial models that included interaction terms and proceeded to additive models with main effects only. Model selection was based on Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham and Anderson 1998). Models where $\Delta AIC_c < 2$ from the best fit model ($\Delta AIC_c = 0$) were considered equally parsimonious. The ratio of AIC_c weights between two models was used to quantify the relative degree that a pair of models were supported by the data (Burnham and Anderson 1998). Annual parameter estimates were calculated using model averaging. We used the variance components procedure in Program MARK to obtain overall estimates of apparent survival that included only process variance only. All parameter estimates (including means) are presented as ± SE unless otherwise noted.

RESULTS

In total, 311 male prairie-chickens (135 yearlings, 176 adults) were captured and banded during the first four years of this study (1998–2001). Forty-six of these birds were treated as not released at last capture because of known mortality events, known movements that led to permanent emigration, and a subset of birds that were collected for a separate study (Robel et al. 2003) of internal parasites. Of the remaining birds, 175 males (93 yearlings, 82 adults) were recaptured at least once (Table 1).

The parametric bootstrap goodness-of-fit test indicated that the global model (ϕ^1_{age*t}, ϕ^{2+}_{t},

TABLE 1. Trapping effort (mean ± SD, *n*) and numbers of yearling and adult Lesser Prairie-Chicken males captured on leks in Finney County, Kansas. Males are distinguished as first encounter (F) or recaptured (R) based on capture history.

			Yearling		Adult	
Year	No. of leks	Trap days per lek	F	R	F	R
1998	6	11.3 ± 1.5, 68	50	—	44	—
1999	8	7.8 ± 4.5, 62	23	15	26	6
2000[a]	20	6.9 ± 1.6, 138	52	11	85	5
2001	19	7.2 ± 0.5, 137	48	36	59	45
2002[b]	19	7.5 ± 1.2, 143	38	31	38	26
Total		7.9 ± 1.7[c], 548	173	93	214	82

[a] Area II was included in trapping effort from 2000–2002.
[b] First captures in 2002 were not used in survival analyses.
[c] This value represents the average trap days per lek for the duration of the study.

p_{age*t}) met the assumptions of mark-recapture analysis (P = 0.63). We did not find evidence of overdispersion so we used AIC$_c$ for model selection and inference. Modeling of recapture probabilities as a function of trapping-effort, time-dependent rates, and a constant recapture rate were equally parsimonious (Table 2). Given that we had only five capture occasions, we constrained capture probabilities to be a function of trapping-effort in all subsequent models (p_e). Our overall estimate of recapture rate was 0.82 ± 0.05.

Model selection based on AIC$_c$ indicated that the best fit model (ϕ^1_{age+t}, ϕ^{2+}_c, p_e) was one with annual variation in apparent survival after first capture, a constant difference between yearlings and adults, and a difference in apparent survival after first capture and returning birds (Table 2). This model was approximately three times more likely supported by the data than the next best fitting model, a model without age-specific variation in apparent survival. Models with annual variation in apparent survival of returning birds (ϕ^{2+}) were not supported by the data (ΔAIC$_c$ > 7).

Model-averaging revealed substantial annual variation in estimates of apparent survival apparent rates of male prairie chickens, with the highest rates during 2000–01 ($\hat{\phi} > 0.6$) and the lowest rates during 1999–2000 ($\hat{\phi} < 0.4$, Fig. 1). Overall estimates of apparent survival were obtained by applying the variance components procedure to an unconstrained model (ϕ^1_{age*t}, ϕ^{2+}_t, p_e). Apparent survival rates of males were ranked: yearlings after first capture ($\hat{\phi}^1_{yr}$, 0.60 ± 0.12) > adults after first capture ($\hat{\phi}^1_{ad}$, 0.44 ±

TABLE 2. Mark-recapture models to determine the effects of age on apparent survival of male Lesser Prairie-Chickens in Finney County, Kansas, 1998–2002. Model fit is described with deviance, the number of parameters (K), the difference in Akaike's Information Criterion corrected for small sample size from the best fit model (ΔAIC$_c$), and AIC$_c$ weights. Model structure estimated apparent survival immediately after banding (ϕ^1), apparent survival in returning birds (ϕ^{2+}), and probability of recapture (p). Factorial models (*) included main effects and their interactions; additive models (+) included only main effects. Model effects include: age = age-class at first capture (yearling vs. adult), t = time-dependence, e = sampling effort, and c = constant model. We report the global model and reduced models with at least minimal support (AIC$_c$ weight > 0.01).

	Model statistics[a]			
Model structure[b]	K	Deviance	ΔAIC$_c$	AIC$_c$ weight
ϕ^1_{age+t}, ϕ^{2+}_e, p_e	8	22.35	0.00	0.63
ϕ_t, p_e	6	28.61	2.12	0.22
ϕ^1_t, ϕ^{2+}_c, p_e	7	29.12	4.70	0.06
ϕ^1_{age*t}, ϕ^{2+}_c, p_e	11	22.26	6.19	0.03
ϕ^1_{age*t}, ϕ^{2+}_t, p_t	14	16.97	7.26	0.02
ϕ^1_{age*t}, ϕ^{2+}_t, p_{age*t}	17	13.82	10.56	0.01

[a] The lowest AIC$_c$ value was 655.41.
[b] The global model for the candidate set was ϕ^1_{age*t}, ϕ^{2+}_t, p_{age*t}.

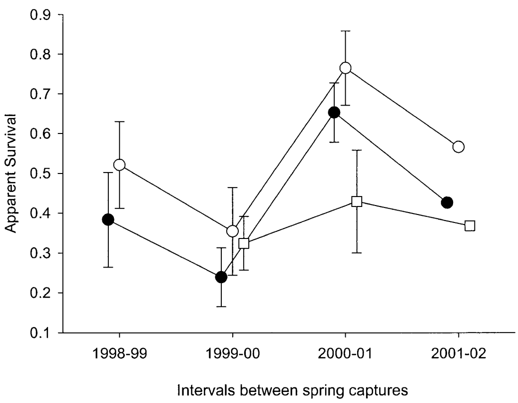

FIGURE 1. Annual variation in apparent survival rates (mean ± SE) of three age-classes of male Lesser Prairie-Chickens: yearlings after first capture (unfilled-circles), adult after first capture (filled-circles), and returning birds (unfilled-squares). Survival rates were estimated using the model averaging procedure in MARK. Because of time dependence in apparent survival and recapture probability in some candidate models, we were unable to estimate the SE (ϕ) for the last interval.

0.10) > returning birds ($\hat{\phi}^{2+}$, 0.36 ± 0.10). In contrast to these apparent survival rates, the probability of site-fidelity among male prairie chickens increased with age. The frequency of males that did not switch leks and were recaptured at the same lek site was significantly lower among yearlings (80%; $n = 60$) than adults (92%, $n = 65$, $G = 4.7$, $P = 0.03$). Among males that switched leks, the distance moved between consecutive years was similar for both yearlings (3.3 ± 0.6 km, $n = 12$) and adults (3.1 ± 0.7 km, $n = 5$, $t = 0.1$, $P = 0.91$).

DISCUSSION

This study provides the first estimates of apparent survival for Lesser Prairie-Chickens from analyses of live encounter data. Our major findings were: 1) apparent survival rates varied considerably among years, 2) age-specific variation in apparent survival was pronounced and declined strongly with increasing age-class, and 3) age-specific declines in apparent survival could be attributed to variation in true survival because fidelity to lek sites increased with male age. The best fit model revealed considerable annual variation in apparent survival, particularly in the interval after first capture. Moreover, the additive term indicated that yearling and adult males were affected by local environmental factors in the same way. These results suggest that estimates of survival from studies lasting ≤3 years should be viewed with caution. Brown (1978) did not measure survival directly, but found that the total numbers of Lesser Prairie-Chickens, and the yearling to adult ratio among harvested birds, were both positively correlated with precipitation in the previous year. Although our 5-year study was longer than most previous Lesser Prairie-Chicken population studies, we did not attempt to model apparent survival as a function of annual covariates because we did not think that estimates of apparent survival for only four intervals was adequate to assess factors affecting annual variation.

Apparent survival is influenced by both true survival and site fidelity. If age-specific declines in apparent survival had been due to site fidelity, then breeding dispersal leading to permanent emigration should have been greater among adults. In fact, the interlek-movement data demonstrated the opposite pattern; yearling males were more likely to switch leks than adults, although both age-classes moved similar distances after switching. Similar results have been reported for other lek-mating grouse (Dunn and Braun 1985, Storch 1997). Thus, the strong age-specific declines in apparent survival among male prairie-chickens indicate age-specific declines in true survival. Furthermore, the age-specific declines in true survival are likely to be even more pronounced than the pattern suggested by our estimates of apparent survival, because movement data indicated that permanent emigration was more likely to occur among yearlings than adults.

The range of our annual estimates of apparent survival encompassed values previously reported for congeneric populations of prairie grouse (Table 3). Direct comparisons among estimates are challenging because a variety of methods have been used to estimate annual survival. Our overall estimate of apparent survival ($\hat{\phi} = 0.45$) improves upon life-table methods and return rates because we controlled for a probability of capture that was less than one ($\hat{p} = 0.82$). Campbell (1972) reported return rates of 0.32 for Lesser Prairie-Chickens in New Mexico, which would yield apparent survival rates that are comparable to our study if capture rates were similar. Adjusting the return rate of Campbell (1972) with our recapture rate provides an estimate of $\hat{\phi} = 0.39$. By using live encounter information

TABLE 3. A review of annual survival rates (mean ± SE, *n*) of male Lesser Prairie-Chickens (*Tympanuchus pallidicinctus*), Greater Prairie-Chickens (*T. cupido*), and Sharp-tailed Grouse (*T. phasianellus*).

Species	Data type[a]	Model type[b]	Survival	Source
Lesser Prairie-Chicken	R	LFT	0.32 ± 0.04, 116	Campbell 1972
	B	CJS	0.45 ± 0.06, 311	This study
	T	K-M	0.57 ± 0.11, 36	Jamison 2000
Greater Prairie-Chicken	B	LFT	0.47 ± 0.01, 1286	Hamerstrom and Hamerstrom 1973
Sharp-tailed Grouse	B	PRP	0.17 ± 0.05, 65	Moyles and Boag 1981
	T	K-M	0.13 ± 0.06, 30	Boisvert 2002
	B	PRP	0.36 ± 0.06, 61	Gratson et al. 1991
	B	LFT	0.50 ± 0.07, 51	Amman 1957

[a] Method of data collection includes: live encounters (B), dead recoveries (R), and radio-telemetry (T).
[b] Survival was estimated using one of the following statistical models: CJS = Cormack-Jolly-Seber, K-M = Kaplan-Meier, LFT = life-table analysis, and PRP = the proportion of birds returning.

from leg-banded birds, we were also able to avoid the restrictive assumptions of estimating survival rates from age ratios in harvest data (Williams et al. 2002), and the potential negative effects of radio-transmitters on survival (Marks and Marks 1987, Burger et al. 1991).

In a review of the literature, we located age-specific estimates of male survival for 14 populations of grouse (Table 4). Differences in annual survival between yearlings and adults did not support our prediction of greater age-structure among grouse that display on leks (range = −0.30 to 0.05, $n = 7$) or dispersed arenas (range = −0.11 to −0.03, $n = 3$), compared to monogamous species (range = −0.19 to +0.01, $n = 4$). Instead, the general pattern was that survival of males declines with age in most grouse species (9 of 14 populations). These patterns differ from other short-lived birds, where survival rates are generally greater among adults than yearlings (Sæther 1990, Martin 1995, Sæther and Bakke 2000).

Yearling male grouse could have higher survival if reproductive effort is lower in this age-class. In Capercaillie (*Tetrao urogallus*), males do not achieve a definitive adult breeding plumage until at least 2 years of age and do not regularly attend leks until 3 years of age (Wegge and Larsen 1987, Storch 1997, 2001). In Greater Sage-Grouse (*Centrocercus urophasianus*), yearling males have lower rates of daily lek attendance and frequently switch lek sites (Emmons and Braun 1984, Walsh et al. 2004), resulting in lower mating success (Wiley 1978, Hartzler and Jenni 1988). In Blue Grouse (*Dendragapus obscurus*), Spruce Grouse (*Falcipennis canadensis*), and Willow Ptarmigan (*Lagopus lagopus*), yearlings are more likely to be non territorial than older birds, although yearlings will occupy vacant territories when territory holders are removed (Lewis and Zwickel 1982, Hannon and Smith 1984, Szuba and Bendell 1988). Predation risk can be substantial for grouse species, regardless of their mating system (Berger et al. 1963, Gibson and Bachman 1992, Thirgood et al. 2000). Greater activity in defense of lek sites or breeding territories may expose older birds to greater predation risk, resulting in lower survival rates. In some species of grouse, declining adult survival could also be the result of contaminants accumulating in body tissues (Pedersen and Myklebust 1993, Larison et al. 2000), although this explanation is unlikely in that a similar pattern exists across all populations of grouse species (Table 4).

In summary, we observed strong annual- and age-dependent effects in the apparent survival of male Lesser Prairie-Chickens. Because yearling males survived at a higher rate than adults, this suggests that competition for mates at lek sites could entail a substantial cost, if older and more dominant males have lower survival as the result of male-male competition. However, our review suggests that age-specific declines in male survival rates are a general feature of grouse demography and are not solely a feature of lek-mating species. In the future, it would be valuable to investigate age-specific variation in both the reproductive effort and survival across a range of grouse species. Stronger tests of the effect of mating system on age-specific survival of grouse will be assisted by better estimates of annual survival based on modern statistical methods.

TABLE 4. A review of published age-specific annual rates (mean ± SE) for male grouse species in relation to their mating system.

Species	Data type[a]	Model type[b]	Male age-class		Source
			1 year	2+ years	
Promiscuous on leks					
Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*)	B	CJS	0.60 ± 0.12	0.43 ± 0.09	This study
Lesser Prairie-Chicken (*T. pallidicinctus*)	B	LFT	0.35 ± 0.04	0.30 ± 0.07	Campbell 1972
Greater Prairie-Chicken (*T. cupido*)	B	LFT	0.50 ± 0.02	0.48 ± 0.03	Hamerstrom and Hamerstrom 1973
Sharp-tailed Grouse (*T. phasianellus*)	B	PRP	0.39 ± 0.08	0.33 ± 0.11	Gratson et al. 1991
Greater Sage-Grouse (*Centrocercus urophasianus*)	B	REC	0.63 ± 0.03	0.37 ± 0.01	Zablan et al. 2003
Black Grouse (*Tetrao tetrix*)[c]	T	K-M	1.00	0.70 ± 0.10	Anglestam 1984
Black-Billed Capercaillie (*Tetrao urogallus*)	W	PRP	0.32 ± 0.13	0.37 ± 0.13	Moss 1987
Promiscuous on dispersed arenas					
Ruffed Grouse (*Bonasa umbellus*)	B	PRP	0.44 ± 0.05	0.41 ± 0.07	Gullion and Marshall 1968
Spruce Grouse (*Falcipennis canadensis*)	B	PRP	0.92 ± 0.03	0.81 ± 0.03	Keppie 1979
Blue Grouse (*Dendragapus obscurus*)	B	PRP	0.70	0.60 ± 0.04	Lewis and Zwickel 1982
Monogamous					
Willow Ptarmigan (*Lagopus lagopus*)	B	PRP	0.44 ± 0.05	0.25 ± 0.05	Bergerud 1970
Rock Ptarmigan (*L. mutus*)	B	PRP	0.24	0.21	Weeden 1965
White-tailed Ptarmigan (*L. leucurus*)	B	LFT	0.76	0.58	Braun 1969
Hazel Grouse (*Bonasa bonasia*)	T	K-M	0.71 ± 0.09	0.72 ± 0.07	Montadert and Leonard 2003

[a] Method of data collection includes: live encounters (B), radio-telemetry (T), and age ratios in wings of harvested birds (W).
[b] Survival was estimated using one of the following statistical models: CJS = Cormack-Jolly-Seber, K-M = Kaplan-Meier, LFT = life-table analysis, PRP = the proportion of birds returning, and REC = recovery models.
[c] Survival estimates for summer breeding season only.

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