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Daily survival rates of ruffed grouse *Bonasa umbellus* in northern Minnesota

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We radio-marked 56 ruffed grouse *Bonasa umbellus* in northern Minnesota, USA, during 1963-1965 and 2001-2002. Of these, we estimated the daily survival rate of 49 individuals (32 females and 17 males; of which 27 were grey phase and 22 were red phase) during the breeding and non-breeding seasons. We investigated whether daily survival varied by age, colour phase, gender, season and transmitter type. A model representing an interaction between colour phase and season fit the data best (AIC_c = 154.760) and was 77% more likely than any of our other *a priori* models. Daily survival rates were identical during the breeding season (0.998; SE = 0.002 for both colour phases), but higher for red-phased (0.994; SE = 0.003) than for grey-phased (0.980; SE = 0.007) birds during the non-breeding season. The daily estimate of grouse survival pooled across all individuals and seasons was 0.994 (SE = 0.002), which yielded an annual survival probability of 0.111 (SE = 0.082). The estimated annual survival rate was 0.010 (SE = 0.132) for grey-phased birds and 0.206 (SE = 0.146) for red-phased birds. There was no difference in survival rates between the two study periods. Our estimated annual survival rates were similar to other rates reported for ruffed grouse.

Key words: Bonasa umbellus, Galliformes, known-fate modelling, radio telemetry, ruffed grouse, survival rate

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The ruffed grouse *Bonasa umbellus* is widespread in North America (Rusch, DeStefano, Reynolds & Lauten 2000). Because it is a favoured game bird, it has been studied for more than 70 years (Rusch et al. 2000). All populations show annual variation in abundance, which may be a reflection of changes in habitat quality, predation rate, hunting pressure, reproduction or weather conditions (Rusch et al. 2000). Most studies of ruffed grouse survival focus on annual or monthly rates. However, estimation of annual or monthly survival may obscure some factors that operate over short time periods. Therefore, we estimate daily survival rates of radio-marked ruffed grouse based on a set of alternative hypotheses in an exploratory analysis to examine some long-held notions of survival in this species.

Material and methods

Study area

We studied ruffed grouse on the Cloquet Forestry Center (1,352 ha; hereafter referred to as Cloquet), northern Minnesota (46° 31'N, 92° 30'E), USA. The forest has been a game refuge since 1924, with the exception of

an experimental ruffed grouse hunt on a portion of the forest in 1961. The climate is characterized by warm, humid summers and cold, dry winters (Tester 1997). Between 1972 and 2002, the average annual precipitation was 800 mm, with 64% of the precipitation falling during the growing season (May-September). Between 1972 and 2002, the average daily low temperature was -18°C during January and the average daily high temperature in July was 27°C. The topography is relatively flat, with elevations ranging from 374 m to 394 m a.s.l.

Cloquet is located in the boreal forest biome. Lowland habitats (e.g. bogs and forested wetlands) occupy approximately 30% of Cloquet, while the remaining 70% consist of upland forests and clearings. Because Cloquet is a research centre, many upland forest stands were experimentally manipulated, which resulted in a complex mosaic of forest types, age classes, stand structures and other vegetation types (e.g. brush fields). Red pine *Pinus resinosa*, aspen *Populus tremuloides* and *P. grandidentata* and jack pine *P. banksiana* are the dominant forest types. Beaked hazel *Corylus cornuta* is the dominant shrub cover in closed-canopy forests. Other common shrubs include Juneberry *Amelanchier* spp., pin cherry *Prunus pennsylvanica*, chokecherry *P. virginiana* and alder *Alnus* spp. Ruffed grouse inhabit most forest zones, particularly aspen, which they use in all age classes and densities.

Field techniques

We captured grouse in mirror and lily pad traps (Gullion 1965). We determined the sex of captured grouse by the number of rump spots (Samuel & Hudson 1989) and the length of a middle rectrix (Davis 1969). We also recorded age (hatch year or after hatch year; Larson & Taber 1980) and colour phase (red or grey). Grouse captured during 1963-1965 were fitted with backpack-style radio transmitters (20 g) developed by Marshall & Kupa (1963) and modified by Brander (1965). Grouse captured in 2001 were fitted with necklace-style transmitters (10-11g, ATS Inc., Isanti, MN). Between 1963 and 1965, the battery was positioned above the crop and the transmitter on the top of the back, whereas in 2001 both were positioned above the crop on radio-marked birds. A 2-element yagi antenna and a portable receiver were used to relocate grouse during 1963-1965 (Marshall & Kupa 1963). A TRX2000S receiver (Wildlife Materials, Carbondale, IL) and a 3-element yagi antenna (ATS, Inc., Isanti, MN) were used during the winter of 2001/2002. During 1963-1965, we recorded the fate (alive or dead) of individual birds once a day. In contrast, we relocated birds twice a week during 2001-2002. When a mortality signal was recorded in the latter sample of grouse, we assumed, for the purposes of analysis, that death occurred at the midpoint between the last day that it was known to be alive and the first day it was known to be dead. If the fates of individuals were unknown due to battery failure or movement off the study area, the individual was censored on the midpoint between the last day it was known to be alive and the first day we either detected a mortality signal or lost radio contact (Winterstein, Pollock & Bunck 2001).

Data analysis

We used an extension of the staggered entry Kaplan-Meier estimator (Pollock, Winterstein, Bunck & Curtis 1989) in program MARK (known-fate models; White & Burnham 1999) to estimate daily survival rates of grouse. Estimating daily survival rates allow the use of radio-marked birds with sparse data and may capture effects due to brief events like severe storms. The program MARK allowed comparison of models with covariates that represented independent hypotheses using model selection techniques. Our approach was to: 1) qualitatively predict the influence of sex, age, season (breeding or non-breeding) and colour phase on survival rates of grouse, 2) express predictions as statistical hypotheses (models), and 3) rank the models' relative ability to fit the data using a small sample adjustment (AIC_c; Hurvich & Tsai 1989, Burnham & Anderson 1998) of Akaike's Information Criterion (Akaike 1973; see model selection below).

Qualitative hypotheses

We developed 10 *a priori* hypotheses based on the literature about the influence of sex, age, breeding season, colour phase and method of radio-transmitter attachment on the daily survival rate of ruffed grouse. We did not include a cycle phase hypothesis because both sampling periods occurred during the low phase of a cycle. We also did not include a hypothesis about the effects of snow on survival because we had no information on snow quality during the early part of the study. Snow quality, rather than amount, would be the appropriate variable to examine. Gullion & Marshall (1968: 141) reported that survival rates of male and female grouse were not different at Cloquet based on colour marking and leg banding. However, one marking technique (back tags) affected survival rates (Gullion & Marshall 1968), which could have confounded gender effects. Given the uncertainty about gender effects on survival, we included a sex-effects model with a prediction that females would have lower survival rates than males. Seasonal differences in ruffed grouse mortality have been observed in other studies (Keith & Rusch 1989, Small,

Holzwart & Rusch 1991). The highest mortality rates occurred during the summer and early fall in Canada (Rusch, Gillespie & McKay 1978) and during the winter in Missouri (Thompson & Fritzell 1989), Wisconsin (Small et al. 1991) and Minnesota (Gullion & Marshall 1968). We predicted that survival would be lower in winter due to winter stress or predation. We also included a hypothesis representing the interaction between breeding season and sex, and predicted that females would have higher mortality rates during the breeding season, but have the same survival rate as males during the non-breeding season. In general, first-year birds have lower survival rates than adult birds, so we included an age model with this prediction. Further, we included a hypothesis representing additive effects of age and gender. We predicted that females would have lower survival rates than males and young birds would have lower survival rates than older birds.

Continental-wide patterns indicated that red-phase birds predominate the southern populations, whereas grey-phased birds predominate the northern populations (Bump, Darrow, Edminster & Crissey 1947). Both colour phases were found at Cloquet, but the percentage of the two colour phases varied among years, with red-phased birds generally being less common (Gullion & Marshall 1968). However, red-phase birds increased in abundance during winters with favourable snow-roosting conditions, but had higher mortality rates during winters with poor snow-roosting conditions. Therefore, we hypothesized that colour phase was associated with daily survival rates of grouse at Cloquet, with red-phased birds generally having lower survival rates. Although the mechanism causing the differential survival between the colour phases is unknown, weather has been suggested as one possible hypothesis (Gullion & Marshall 1968). Therefore, we also included a model with an interactive effect between colour phase and season. Specifically, we predicted that red-phased birds would have higher survival rates than grey-phased birds during low cycle years and years with low snowfall (Gullion & Marshall 1968, Gullion 1981) as occurred during our study. We proposed this hypothesis under the assumption that grey birds will be more cryptic on snow-covered ground. However, we were unsure of the predicted relationship of colour phase and survival during the breeding season. Another model represented additive effects of colour phase, gender and age.

We included two models using transmitter type as a categorical covariate because a critical assumption of the Kaplan-Meier method is that the transmitters do not cause mortality. While these models do not evaluate transmitter effects on birds (i.e. they depict differences between transmitter types), a top model including transmitter would indicate that this assumption was violated. However, this model was confounded by time (e.g. two study periods). Thus a model that was supported by the findings could also indicate that habitat conditions, predator density or weather conditions varied between study periods. If the transmitter model was not supported, we still could have violated the assumption that the transmitters did not cause mortality, even if the different transmitter types were not confounded with other factors. We also included a transmitter type by season interaction model to explore seasonal effects of transmitter type and sampling design (e.g. a higher proportion of necklace-style radios were used during the non-breeding season than the breeding season, and Small & Rusch (1985) noted a negative effect of transmitter attachment in the non-breeding season). We developed one final model, an 'intercept only' model (Table 1), which depicts a constant survival rate among all birds and across seasons.

Table 1. Results of AIC_c model selection for factors influencing survival rates of ruffed grouse in northern Minnesota, USA, during 1963-1965 and 2001-2002.

Model	# Parameters	AIC_c	ΔAIC_c	AIC_c Weight
Season * Colour phase	4	154.760	0.000	0.768
Colour phase	2	159.347	4.587	0.078
Sex + Colour phase + Age	4	160.001	5.241	0.056
Season	2	160.534	5.774	0.043
Sex	2	161.964	7.204	0.021
Intercept only	1	162.177	7.417	0.019
Transmitter type	2	163.256	8.496	0.013
Age	2	163.916	9.156	0.010
Sex + Age	3	163.966	9.206	0.010
Season * Transmitter type	2	164.564	9.804	0.000
Season * Sex	4	225.602	70.842	0.000

Developing quantitative models

We used the Kaplan-Meier estimator because it does not assume constant survival for the duration of the study (Winterstein et al. 2001). This estimator can be extended to incorporate individual covariates (e.g. age, gender or colour phase) with a link function in a binomial model (Pollock 2002). For example, the structure of an age model would be:

$$S_{age} = \frac{1}{1+e^{-(\beta_0+\beta_1 \cdot X_{age})}}$$

where S_{age} = estimated probability of surviving a day at a given age, β_0 = intercept, β_1 = slope parameter for age, and X_{age} = an indicator variable that is 0 for hatch year individuals or 1 for after hatch year individuals (Franklin 2000).

Model selection

We used model selection based on information theory to rank our *a priori* hypotheses (Burnham & Anderson 1998). We used AIC_c weights, 95% confidence intervals and standard errors to estimate the absolute strength of our conclusions. AIC_c weights can be used to interpret the relative likelihood of models given the suite of models (Burnham & Anderson 1998). The 95% confidence intervals of parameter estimates that do not include zero represent strong correlations, whereas those that include zero indicate weak or no correlations for those particular variables. We presented standard errors to indicate the precision of back-transformed estimates. For example, we used the delta method to estimate the standard error of annual and seasonal daily survival probabilities.

Results

We captured and radio marked 44 ruffed grouse during February 1963 - August 1965, and an additional 12 in 2001. However, three individuals were eliminated from the 1963-1965 sample and four were eliminated from the 2001 sample because the radios either failed immediately after release of the birds or the birds were preyed upon quickly. Thus, we used 49 individuals (32 females and 17 males) in this analysis. Grouse were monitored for an average of seven weeks (range: 2-17 weeks). Our best model for estimating daily survival rates was an interaction between colour phase and season (see Table 1). This model indicated that survival rates were similar for both colour phases during the breeding season (0.998, SE = 0.002), but that daily survival was lower for grey-phase (0.980, SE = 0.007) than red-phase (0.994, SE = 0.003) birds during the non-breeding season. The AIC_c weight for this model was high, indicating that this model was 77% more likely to fit the data than the other models (see Table 1). Parameter estimates indicated that due to the main effect of colour phase, red-phased birds had a higher probability of annual survival than grey-phased birds (95% confidence interval for colour phase did not include zero; Table 2). Although season was in the top-ranked model, the 95% confidence interval included zero. Therefore, there was no clear correlation between season and daily survival. Transmitter type did not improve the model fit. The model representing a main effect of transmitter types, which fit better than the interaction between transmitter type and season, was > 5 AIC_c points higher (lowest AIC_c is best model) than the season*colour phase model. The intercept only model indicated that the daily survival rate was 0.994 (SE = 0.002), which yielded an annual estimate of 0.111 (SE = 0.082) when extrapolated.

We raised the daily survival estimates for each colour phase to the power of 153 for the breeding season (red phase = 0.736, SE = 0.226; grey phase = 0.736, SE = 0.226) and 212 for the non-breeding season (red phase = 0.279, SE = 0.179; grey phase = 0.014, SE = 0.417) to estimate seasonal survival rates. We also multiplied the seasonal survival rates for each colour phase to estimate an annual survival rate. The colour phase by season interaction model indicated that the annual survival rate for grey-phased birds was 0.010 (SE = 0.132), and the annual survival rate for red-phased birds was 0.206 (SE = 0.146).

Table 2. Beta parameter estimates for AIC_c selected model (Season * Colour phase) for predicting daily survival of radio-marked ruffed grouse in northern Minnesota. Season is treated as binary indicator variable with 0 = non-breeding season (1 September - 31 March) and 1 = breeding season (1 April - 31 August), and colour phase is treated as binary indicator variable with 0 = red/brown phase and 1 = grey phase.

		95% Confidence intervals	
Parameters	Beta estimates (SE)	Lower	Upper
Intercept	5.128 (0.486)	4.175	6.080
Season	0.875 (0.801)	-0.694	2.445
Colour phase	-1.229 (0.531)	-2.269	-0.189
Colour phase * Season	1.585 (0.813)	-0.009	3.179

Discussion

Although grouse daily survival rates were high, annual survival probability of ruffed grouse in our study was lower than other estimates of annual survival calculated from radio-marked ruffed grouse (0.111 vs 0.18 in Small et al. (1991) and 0.35 in Thompson & Fritzell (1989)). The only other published estimate of daily survival rates is from an introduced population in northern Missouri, which had a lower estimate (0.986 in Kurzejeski & Root 1988) than our study (0.994). We do not know if these differences were biologically significant as different estimation techniques, habitat, weather conditions, predator density, phase of cycle or sampling variance precluded a direct comparison.

Our analysis was consistent with our *a priori* predictions because both the first and second study period coincided with below average snowfall and low points in the cycle. Several hypotheses have been proposed to explain the frequency and distribution of colour phases in populations of ruffed grouse (Gullion & Marshall 1968, Gullion 1981). In general, grey-phased birds numerically dominate northern populations, whereas red-phased birds dominate southern populations, which

suggests a climate-related response. However, Gullion & Marshall (1968) and Gullion (1981) hypothesized that colour phases vary in frequency as a result of winter weather conditions, phase of the population cycle and presence of goshawks *Accipiter gentilis*, but the actual causative mechanism remains unknown. Our results are consistent with red-phased birds having a cryptic colour advantage (*cf.* the Cryptic Advantage Hypothesis). That is, the majority of birds monitored during the non-breeding season came from the 2001 sample, when snow cover was absent or patchy during most of the winter. In this case, our results implied that darker-coloured birds may have been more cryptically coloured relative to habitat conditions during the non-breeding seasons of our study, and hence may have avoided predation more effectively than lighter-coloured grey birds. Thus, one hypothesized scenario could be that red-phased birds have higher survival rates when snow is absent or patchy, grey-phased birds have higher survival when snow is present but not available for snow roosting, and both colour phases do well when snow roosts are available. If this was true, then our results did not support a cold-adapted hypothesis as an explanation for colour phase variation because red-phased birds, which should have had lower survival rates than the supposedly cold-adapted grey birds during the winter, survived at higher rates than grey birds during the non-breeding season (i.e. our results contradict the cold-adapted prediction).

Because we lack key information (e.g. snow depth and quality, density and distribution of goshawks or other predators) about the conditions under which some birds were monitored, we believe our suite of models is incomplete. In fact, we predict that future studies incorporating larger samples, longer time periods and additional data (e.g. on ice storms and snow quality) will almost certainly alter our preliminary inferences about factors associated with survival rates. Nevertheless, we feel our analysis provides a template upon which future studies should explore ecological relationships using biologically-based models and response variables related to fitness. Despite its limitations, our approach illustrates the value of modelling survival on temporal scales shorter than an annual scale. Our results support a general hypothesis that colour-phase may be related to adaptive colouration during various weather conditions.

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