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Source: Wildlife Biology, 15(1) : 60-67

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/07-087

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Wildl. Biol. 15: 60-67 (2009)
DOI: 10.2981/07-087
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Original article

Factors influencing the survival of neonate sharp-tailed grouse *Tympanuchus phasianellus*

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Offspring survival after leaving the nest is a critical element of population viability and in the management of game species. We estimated brood survival to 35 days and examined the factors thought to influence individual chick survival during the first two weeks post-hatching in a population of sharp-tailed grouse *Tympanuchus phasianellus* near Fort St. John, British Columbia, Canada, during 2004-2005. Using program MARK and an information-theoretic approach, we assessed the importance of female attributes, date of hatching, distance moved from the nest and weather conditions experienced prior to hatching and during brood-rearing for survival of offspring. During 2004-2005, 67% of broods had at least one chick that survived to 35 days of age, but within these broods only 34% of the chicks survived. Later hatching dates were positively related to survival during the 0-14 day age interval, whereas the distance moved from the nest by a brood and inclement weather conditions during the first seven days post-hatching significantly reduced the survival rate of chicks to 14 days of age. Further, inclement weather prior to hatching was positively related to the survival of offspring to 14 days, perhaps because wet weather created favourable foraging environments and habitat characteristics during brood rearing. Cohesive management of nesting and brood-rearing habitats is required to reduce offspring mortality associated with increased travel between suitable habitats, and may minimize mortality during periods when weather is unfavourable.

Key words: British Columbia, brood movements, brood success, chick survival, program MARK, radio-telemetry, Tympanuchus phasianellus, weather

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Received 14 November 2007, accepted 23 May 2008

Associate Editor: Hannu Pöysä

Success during the nesting period is one of the most important factors affecting reproductive success and population growth in birds (Bergerud 1988, Hudson & Rands 1988). However, offspring survival after leaving the nest is also a critical element of population viability and management of species (Aldridge & Brigham 2003, Panek 2005). Relatively little information exists on the factors affecting survival of avian offspring after nest departure, largely because of the difficulty in accurately measuring survival of chicks and determining sources of mortality in secretive and mobile species (Johnson et al. 1992, Rotella & Ratti 1992). Survival of precocial offspring is, however, often most influenced by chilling from inclement weather or poor female attentiveness, predation or starvation (Bergerud 1988, Johnson et al. 1992).

In precocial species such as grouse, chicks are susceptible to environmental conditions because of their inability to thermoregulate until approximately

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eight days of age (Erikstad & Spidsø 1982). Poor weather conditions experienced during the hatching period can directly result in mortality of chicks and even complete brood loss (Flanders-Wanner et al. 2004). Chicks may also starve during poor weather, as cool and wet conditions result in increased time spent brooding and, therefore, less time spent foraging (Erikstad & Spidsø 1982, Erikstad 1985). In addition, weather conditions can indirectly affect offspring survival by influencing the abundance and availability of insects, which are the primary food of gallinaceous chicks through their first week of life (Erikstad 1985). Habitat conditions can also affect survival of chicks by creating suitable foraging environments and high-quality cover characteristics that allow them to avoid predation (Bergerud 1988, Hagen et al. 2005), which is likely the ultimate cause of most offspring mortality in gallinaceous and waterfowl species (Riley et al. 1998, Pietz et al. 2003).

Populations of sharp-tailed grouse *Tympanuchus phasianellus* in the Peace River region of northeast British Columbia, Canada, are thought to have been decreasing over the past several decades, but the cause of this decline is unknown (British Columbia Ministry of Environment, unpubl. data). Our specific objectives were to: 1) measure the success of broods of sharp-tailed grouse from hatching until independence, 2) determine survival rates of individual chicks at various ages during brood rearing, and 3) identify the importance of female body condition and age, weather conditions, hatching date and brood movements for survival of individual offspring.

Material and methods

Study area

Our study was conducted in a 320-km^2 area located approximately 35 km southeast of Fort St. John, British Columbia, Canada, and encompassed the upland areas and river breaks at the confluence of the Beatton and Peace Rivers (56°11'N, 120°25'W; ca 600 m a.s.l.). The study area was located in the Aspen Parkland Ecoregion (Meidinger & Pojar 1991), although much of the area had been converted to agricultural land use including cereal crops, a variety of hay crops and pasture-land for livestock. Aspen *Populus tremuloides* forests, mixed aspen-white spruce *Picea glauca* forests, and black spruce *Picea mariana* muskeg bogs exist in patches amongst large-scale agricultural developments. Along the south and west-facing river breaks, there was a strong influence of natural shrub and grassland communities. Sharp-tailed grouse were reasonably abundant, and multiple lek sites existed in the study area.

Field techniques

During April-May of 2004 and 2005, we captured sharp-tailed grouse on nine different leks throughout the study area using walk-in traps (Schroeder & Braun 1991). All females captured were fitted with 15-g, necklace-style radio transmitters (Model RI-2BM, Holohil Systems Ltd., Carp, ON). We recorded body mass and length of the wing chord for each bird, and used the residuals from a reduced major axis regression of mass against length of wing chord as an index of female body condition (Green 2001). Females were aged as either in their second year (SY) or after-second year (ASY), based on the shape and degree of fraying of the ninth and tenth primary feathers (Bihrle 1993).

We located nests by flushing each marked female on a weekly basis until a nest was found. To estimate date of hatching, we recorded stage of incubation using field candling techniques (Weller 1956). We considered a nest successful if we observed evidence of detached shell membranes, indicating that a minimum of one egg had hatched (Klett et al. 1986). Once eggs hatched, we estimated the survival of chicks by flushing females and their broods on a weekly basis from age seven to 35 days. Beyond 35 days of age, the likelihood of chick dispersal from the brood increases, and quantifying survival past this age may provide biased information as dispersal could be mistaken as chick mortality. We assumed that chicks not observed during a flush count were dead, but because not all chicks may take flight, our measures of survival of individual chicks represent the most conservative estimate of the number of chicks alive.

Data analyses

We used two measures of offspring survival in our analyses. First, we examined overall brood success, defined as the proportion of broods with a minimum of one chick alive, for the entire brood-rearing period (i.e. from hatching to 35 days of age). We examined the effects of year, age of the female and nest attempt on final brood success of 27 broods using the G-test of independence (Sokal & Rohlf 2001). As no female had two broods in one season, we were able to use broods from both first nests and renests without

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Table 1. Descriptive statistics of individual covariates included in models to assess survival of sharp-tailed grouse chicks during the 0-14 day interval in northeast British Columbia during 2004-2005.

	Mean		Range	
Covariate	$\bar{x}$	SE	Minimum	Maximum
Female body condition (residuals)	2.94	8.01	-94.84	76.13
Hatching date (Julian days)	170.78	2.55	158.00	202.00
Distance from the nest during 0-7 day interval (km)	0.52	0.08	0.04	1.32
Pre-hatching weather conditions (PC1 scores)	0.08	0.09	-0.61	1.31
Weather conditions during 0-7 day interval (PC1 scores)	-0.11	0.10	-0.85	0.85

committing pseudoreplication. Two females were monitored over consecutive breeding seasons, and as such, contributed brood-rearing data in both study years. We included data from both years for these females in our analyses, as our results did not change qualitatively compared to when data were analyzed with only one brood from each female.

Second, we examined the survival of 234 individual chicks in 22 broods from hatching to 35 days of age. We first tested whether variability existed in chick survival with respect to brood age and year using the known-fate model and logit-link function in program MARK (White & Burnham 1999, Paasivaara & Pöysä 2007). Our candidate model set included four models: 1) $S_{(\text{brood age})}$, 2) $S_{(\text{brood age})(\text{year})}$, 3) $S_{(\text{year})}$, and 4) $S_{(\text{constant})}$. We used four intervals in our analysis (0-14, 15-21, 22-28 and 29-35 days). Because chicks are flightless at seven days of age and rely on surrounding vegetation for concealment (Hagen et al. 2005), we were unable to accurately count the number of surviving chicks at seven days of age. Therefore, we assessed survival for the period 0-14 days, at which time chicks can be counted as they take flight (Haulton 1999). Differences in sample sizes between analyses of brood and chick survival were due to missing individual covariate data for five broods, which were excluded from chick survival analyses to maintain consistency when comparing models (White & Burnham 1999).

Although some mortality was observed in the 15-21 and 29-35 day intervals (see below), the number of chicks that died in each of these intervals was relatively small (17 and four chicks, respectively). We therefore chose to focus further analyses on survival through the first two weeks post-hatching (0-14 days). We again used the known-fate model and logit-link function in program MARK (White & Burnham 1999, Paasivaara & Pöysä 2007). We developed 23 *a priori* candidate models that included all two-way additive combinations of female age, female body condition, date of hatching, distance a brood moved from the nest site during the first seven days post-hatching, and two weather variables (Table 1). Distance moved was estimated as the straight-line distance from the nest site to the location of the brood at the seventh day flush count using a geographical information system. Our weather variables encompassed two periods hypothesized to influence chick survival: 1) pre-hatching weather conditions and 2) weather conditions during the first seven days of life. We hypothesized that weather conditions experienced 10 days prior to hatching would indirectly affect the survival of offspring by influencing the abundance and availability of forage and habitat conditions after hatching (Flanders-Wanner et al. 2004). In addition, we chose to model weather conditions during the 0-7 day interval because evidence suggests precocial chicks are most susceptible to inclement weather conditions during the first seven days post-hatching (Mendenhall & Milne 1985, Steen et al. 1988). Daily weather data (mean daily temperature, mean daily rainfall and total daily hours of rain) were obtained from the nearest Environment Canada weather station (Fort St. John Airport; Environment Canada 2006), located approximately 35 km northwest of the study area. Due to correlations among the three weather variables, we used principal components analysis (PCA) to generate a single measure of weather for each day of the study period. We defined the study period as beginning 10 days prior to the earliest nest initiation date and ending when the latest brood was 35 days of age in each year, a period of 227 days, pooling data from 2004 and 2005. The first component (PC1) explained 61.7% of the variation, an acceptable value for 3 eigenvalues (Frontier 1976, Jackson 1993). PC1 was positively correlated with mean daily rainfall ($r = 0.94$, $N = 227$) and total hours of rain ($r = 0.94$, $N = 227$), and was negatively related to mean daily temperature ($r = -0.29$, $N = 227$). Therefore, positive PC1 values generally represented cool and wet weather conditions. We averaged PC1 values for the 10-day period prior to hatching and the 7-day period post-hatching for each brood.

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To determine which candidate models best explained variation in the survival of chicks in both sets of analyses (overall, and during the 0-14 day interval), we compared the models using Akaike's Information Criterion corrected for small sample sizes and overdispersion in the data ($QAIC_c$; Burnham & Anderson 1998). Overdispersion can be caused by within-brood dependency, resulting in underestimation of the true sampling variance (Pelayo & Clark 2003). To compensate for overdispersion, we estimated the variance inflation factor ($\hat{c}$) by performing 1,200 parametric bootstrap simulations on the $S_{(brood\ age)}$ model using the median $\hat{c}$ test in program MARK (White & Burnham 1999). The estimated $\hat{c}$ (2.80 ± 0.22) was used for adjusting AIC_c values during model selection. For analyses of survival during the 0-14 day interval, each variable was equally represented in the candidate model set, so we summed the Akaike weight of each model containing the variable of interest to assess the relative importance of each individual variable (Burnham & Anderson 1998, Gunnarsson et al. 2006). We report means $\pm$ 1 standard error.

Results

Brood success, estimated as the proportion of broods with a minimum of one chick alive at 35 days of age, was 0.67 ± 0.09 (N = 27) during 2004-2005. Brood success was not significantly different between years (G = 0.38, df = 1, P = 0.54), first or renest attempts (G = 0.38, df = 1, P = 0.54) or between second-year (SY) or after second-year (ASY) females (G = 0.92, df = 1, P = 0.34). Complete brood loss, where no chicks remained alive at 35 days of age, occurred in six broods (74 chicks; 39.78% of all chick mortality) over the two years, with three broods lost in the first seven days post-hatching, and an additional three broods lost during 8-14 days of age.

Although 67% of the broods were successful, the proportion of chicks surviving to independence was relatively low (0.34 ± 0.07). Over the two study years, 283 chicks were hatched from 27 nests in our study area. Only 97 of these chicks were confirmed to survive to 35 days of age, for an average of 3.59 ± 0.71 chicks per successfully nesting female (N = 27).

Four 'main effects' models were tested to determine the effects of brood age and year on the survival of chicks over the four brood-age intervals. The top model explaining chick survival was $S_{(brood\ age)}$ (Table 2). The rate of chick survival was lowest (0.63 ± 0.04) during the 0-14 day interval and greatest during the 22-28 day interval (0.94 ± 0.05; Fig. 1), and did not differ between years (see Table 2).

We tested 23 covariate models for their influence on the mean survival rate of chicks during the 0-14 day interval. Three models had $\Delta QAIC_c$ scores ≤ 2.0 (see Table 2). Beta-values from these highest-ranking models suggested that increasingly inclement weather conditions experienced during the first seven days after hatching ($\beta = -2.18$, SE = 0.39, 95% CI = -2.95, -1.41) and the distance moved from the nest ($\beta = -1.04$, SE = 0.37, 95% CI = -1.78, -0.31) were both negatively associated with survival of chicks during the 0-14 day interval. Conversely, the rate of

Table 2. Quasi-Akaike's Information Criterion ($QAIC_c$; $\hat{c} = 2.80$) rankings for models of main effects, indicating the rate of survival over all age intervals, and top-ranked ($\Delta QAIC_c \leq 2.0$) covariate models, estimating survival over the 0-14 day interval for sharp-tailed grouse chicks in northeast British Columbia during 2004-2005. Effective sample size was consistent among all candidate models (N = 234).

Model	K[a]	$QAIC_c$	$\Delta QAIC_c$	w_i[b]	Deviance[c]
Main effects models					
$S_{(brood\ age)}$	5	173.12	0.00	0.94	2.65
$S_{(brood\ age)(year)}$	9	178.74	5.63	0.06	0.00
$S_{(constant)}$	2	186.33	13.22	<0.01	21.98
$S_{(year)}$	3	187.47	14.36	<0.01	21.09
Covariate models					
$S_{(hatch\ date + weather\ during\ 0\text{-}7\ day\ interval)}$	4	96.49	0.00	0.32	88.31
$S_{(hatch\ date + pre\text{-}hatch\ weather)}$	4	96.90	0.41	0.26	88.72
$S_{(distance\ from\ the\ nest\ during\ 0\text{-}7\ day\ interval + weather\ during\ 0\text{-}7\ day\ interval)}$	4	98.35	1.86	0.12	90.18

[a] Number of parameters in the model.

[b] Generalized Akaike weights that can be interpreted as the relative degree of certainty associated with each model.

[c] Deviance is defined as the difference in the -2(log-likelihood) of the current model and the -2(log-likelihood) of the saturated model (White & Burnham 1999). In known-fate models of program MARK, deviance cannot be estimated for the most saturated model as the -2(log-likelihood) for the saturated model is the same as the -2(log-likelihood) for the $S_{(group)(time)}$ model (White & Burnham 1999).

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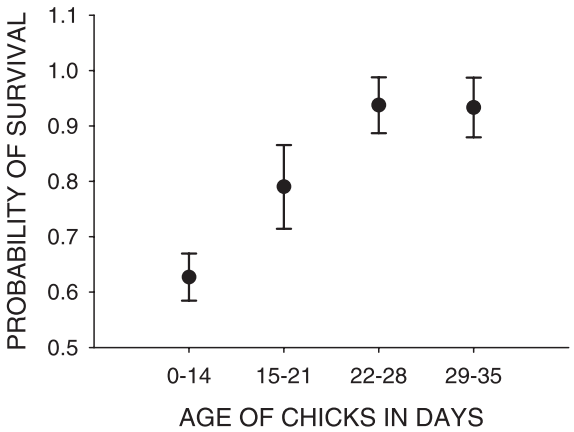


Figure 1. Probability (± SE) of survival of 234 sharp-tailed grouse chicks during four age intervals (0-14 days, 15-21 days, 22-28 days and 29-35 days) in the Peace River region, northeast British Columbia during 2004-2005.

survival was positively related to the date of hatching ($\beta = 0.06$, SE = 0.02, 95% CI = 0.03, 0.09) and to pre-hatching weather conditions ($\beta = 2.86$, SE = 0.52, 95% CI = 1.84, 3.89). The relative importance of each variable, as indicated from the summation of Akaike weights across models, was: weather during 0-7 day interval (0.71), hatch date (0.61), pre-hatching weather conditions (0.35), distance moved from the nest during the 0-7 day interval (0.16), female body condition (0.12) and female age (0.06).

Discussion

Approximately 67% of sharp-tailed grouse broods in our study area had at least one chick alive at independence in 2004 and 2005. This estimate is high compared to many other estimates of brood success reported in studies of upland game birds and waterfowl. For example, estimates of brood success for mallards *Anas platyrhynchos* ranged from 34% to 70% over different years, and averaged approximately 49% (Rotella & Ratti 1992). Conversely, estimates for gadwalls *Anas strepera* were approximately 84% to 30-days of age (Pietz et al. 2003). The first 14 days after hatching are the most critical for survival of precocial offspring (Bergerud 1988, Myrberget 1988), and we found that brood mortality and complete loss of sharp-tailed grouse broods was greatest during the first 14 days post-hatching. Similar brood success rates during the first week post-hatching have been reported for ruffed grouse *Bonasa umbellus*, where approximately 33% of broods were lost during the first seven days, accounting for 42% of total brood loss from hatching to independence (Haulton 1999). An inability to thermoregulate and, in the case of grouse, fly until approximately 8-10 days of age increases the susceptibility of precocial offspring to predation and adverse weather conditions (Bergerud 1988).

Only 34% of sharp-tailed grouse chicks survived to 35 days of age in our study area. This estimate represents the lowest possible survival rate, given the difficulty in accurately counting all chicks during flush counts. Average survival of gallinaceous offspring from hatching to independence has been estimated at 56% (Bergerud 1988). In studies of ruffed grouse, willow ptarmigan *Lagopus lagopus lagopus* and grey partridge *Perdix perdix*, chick survival to independence ranged from 11% to 71% (Myrberget 1988, Panek 1992, Haulton 1999). Survival of sage-grouse *Centrocercus urophasianus* chicks to 50 days of age in Washington was 33% (Schroeder 1997), which is comparable to estimates for sharp-tailed grouse in our study area.

Our results suggest that survival of chicks during the 0-14 day interval increased as weather occurring 10 days prior to hatching became increasingly poor, whereas survival decreased with inclement weather during the first seven days post-hatching (see Table 2). Weather conditions are one of the most important factors affecting chick survival, and are often regarded as the primary explanation for annual variation in survival of offspring (Blank et al. 1967, Panek 1992). Pre-hatching weather conditions can influence chick survival by positively influencing habitat conditions (Erikstad 1985). For example, wet conditions experienced prior to hatching may create more densely vegetated areas, which generally support a greater abundance and diversity of insects (Erikstad 1985, Park et al. 2001) as well as improved cover characteristics (Erikstad 1985, Bergerud 1988). Soil moisture during the months leading up to the peak-hatching period has been positively correlated with offspring survival of grouse, as soil moisture likely increases vegetation growth, thus providing critical cover for young (Bergerud 1988). Further supporting this finding, cumulative precipitation measured from January to July was significantly associated with greater juvenile:adult ratios in the fall for prairie grouse *Tympanuchus* spp., indicative of higher rates of chick survival (Flanders-Wanner et al. 2004). We believe that wet weather leading up to hatching may be critical in creating favourable conditions that increase the phenological development of plants

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that are important to precocial chicks for both cover and as a food source, by supporting greater numbers of insects (Bergerud 1988, Park et al. 2001).

Weather conditions can, however, affect chick survival differently before hatching as compared to after hatching (Steen et al. 1988). Precipitation experienced during the peak-hatching period, particularly during the month of June, is often negatively correlated with offspring survival (Steen et al. 1988, Panek 1992, Flanders-Wanner et al. 2004). This trend was apparent in the survival of sharp-tailed grouse chicks in our study area (see Table 2). During the 0-14 day post-hatching interval, rates of offspring survival were lowest and complete brood loss was the highest, and our results suggest a negative association between chick survival during the first two weeks post-hatching and weather conditions experienced during the 0-7 day interval. Similar results have also been reported for other species of waterfowl and grouse (Mendenhall & Milne 1985, Steen et al. 1988).

Cool and wet weather during the first week of life can directly affect chick survival through increased cooling and wetting when chicks are unable to thermoregulate, resulting in direct chick mortality, and increased stress, energetic demands and predation risk, as many predators actively hunt during periods of adverse weather (Mendenhall & Milne 1985). Weather can also indirectly affect survival of offspring by influencing the amount of time that chicks need to be brooded by the hen (Erikstad & Spidsø 1982). Prolonged brooding can result in a reduction of the amount of time chicks spend foraging, and thus can lead to starvation (Erikstad & Spidsø 1982, Panek 1992, Roersma 2001). Weather may also indirectly affect insect abundance and availability, as insect activity is often lessened during cool and wet weather (Green 1984, Panek 1992). Increased survival of chicks in two species of partridge was directly associated with increased temperatures during June and July, which resulted in more favourable conditions for young chicks as well as increased density and activity of arthropods (Green 1984).

In addition to cool and wet weather conditions, the distance moved from the nest by broods of sharp-tailed grouse during the first week post-hatching was negatively associated with chick survival during the 0-14 day interval (see Table 2). Movement during the brood-rearing period is common in galliformes and some species of waterfowl (Erikstad & Spidsø 1982, Seymour & Jackson 1996). Broods that travel generally have decreased survival (Leonard et al. 1996, Seymour & Jackson 1996) and rates of growth (Mainguy et al. 2006) compared to more sedentary broods. Large-scale movements between brood-rearing areas can result in decreased time spent brooding and foraging (Erikstad & Spidsø 1982), an increased likelihood of chick abandonment (Leonard et al. 1996) and predation (Duncan 1983, Leonard et al. 1996), and increased energetic demands (Mendenhall & Milne 1985, Leonard et al. 1996), all of which can result in increased mortality.

Although we cannot ascertain why sharp-tailed grouse broods moved during the first week after hatching, we observed that some broods moved away from nesting areas, generally located in shrub-steppe habitats, to more agriculturally-dominated areas that appeared to be better suited for brood-rearing. In our study area, some of the most important nesting habitat, in the form of shrub-steppe complexes, occurs in small, isolated patches that are relatively detached from suitable brood-rearing habitats. Nesting areas isolated from suitable brood habitats may be 'sinks' that can result in low brood success and chick survival, as broods can suffer losses when travelling to more desirable brood-rearing areas (Seymour & Jackson 1996, Aldridge 2005). The pattern in which a female selects a nest site (Leonard et al. 1996) combined with isolated nesting areas (Seymour & Jackson 1996) may result in greater brood movements, contributing to decreased survival of neonate sharp-tailed grouse in our study area. Nonetheless, we also observed that broods, which hatched in agricultural areas with good vegetative cover, still made large-scale movements away from the nest site. Further research is required to fully understand the proximate causes of movement of broods on the survival of offspring.

Hatching date was also an important variable influencing the survival of chicks. Decreased success among later-hatching offspring is a common pattern exhibited by a diverse array of temperate-breeding bird species (Verhulst & Nilsson 2008). Our results, however, suggested that sharp-tailed grouse hatching later in the season had higher survival than early offspring. Similar results were reported by Dawson & Clark (1996) for lesser scaup *Aythya affinis* ducklings, which they attributed to seasonally increasing food abundance that enhanced survival of later-hatched ducklings. Seasonal changes in food abundance, as well as weather conditions, may also be responsible for higher survival of late-hatching grouse in our study. Despite the apparent survival advantage of later hatching in lesser scaup, Dawson &

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Clark (2000) subsequently showed that late ducklings had slower rates of growth and reduced rates of recruitment to the breeding population in comparison to early hatched young. Unfortunately, we did not individually mark each chick, so we could not determine the fitness consequences of hatching date for sharp-tailed grouse.

Conclusions

It is apparent that date of hatching, weather conditions and distance moved from the nest are important determinants of the survival of offspring. Although weather conditions cannot be controlled, management practices should be used to enhance habitats that create a greater abundance and availability of insects as well as increased cover to maximize survival of chicks (Bergerud 1988, Park et al. 2001). Further, we suggest that nesting and brood-rearing habitats be managed cohesively to decrease the likelihood of chick and brood mortality experienced during large-scale movements away from the nest.

Acknowledgements - we thank M.P. Gillingham, V.R. Peck, D.L. Heard and anonymous reviewers for comments on previous versions of this manuscript. Financial support for this project was provided by the Habitat Conservation Trust Fund (HCTF) and the Northeast Wildlife Fund. A.D. Goddard was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC) through a Canadian Graduate Scholarship. Research funding was also provided by NSERC and the University of Northern British Columbia through grants to R.D. Dawson. We thank C.J. Goddard, J. Woods and British Columbia Ministry of Environment staff, specifically M. Rowe, R.B. Woods and R.B. Backmeyer, for their assistance in field activities.

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