GRASSLAND HABITAT AND REPRODUCTIVE SUCCESS OF RING-NECKED PHEASANTS IN NORTHERN IOWA

WILLIAM R. CLARK

Department of Animal Ecology Iowa State University Ames, Iowa 50011 USA

TODD R. BOGENSCHUTZ

Iowa Department of Natural Resources Boone, Iowa 50036 USA

Abstract.—We used radio telemetry from 1990–1994 to compare reproduction of 185 female pheasants in a diverse landscape with 25% perennial grassland habitat in Palo Alto County, Iowa, with that of 72 pheasants on an intensively farmed landscape with 9% grassland in Kossuth County, Iowa. Median dates of the beginning of incubation of first nests were almost identical on the areas, but median incubation date of renests was earlier at Palo Alto (22 June) than at Kossuth (5 July). Mean clutch size in first nests was 12.6 eggs, which was greater than clutch size of 9.9 for renesting attempts. Success of first nests was 57.3% at Palo Alto and 44.8% at Kossuth, whereas success of renests was 45.6% at Palo Alto but only 26.9% at Kossuth. Linear logistic regression revealed that nest success averaged 62.3% in undisturbed blocks of habitat such as CRP versus 44.8% in small, linear, or disturbed habitats, regardless of the study landscape. Hen success averaged 70.6% at Palo Alto and 52.2% at Kossuth, and it varied more among years at Kossuth. Pheasant nest success was higher in a diversified agricultural landscape with large blocks of undisturbed habitat. When nesting is restricted to small or disturbed habitat fragments pheasant reproduction is probably reduced enough to limit the potential rate of population increase.

HABITÁCULO HERBÁCEO, Y ÉXITO REPRODUCTIVO DE PHASIANUS COLCHICUS EN EL NORTE DE IOWA

Sinopsis.—Usamos radiotelemetría entre 1990 y 1994 para comparar la reproducción de 185 hembras de Phasianus colchicus en un área diversa con un 25% de herbáceas perennes en el Condado de Palo Alto, Iowa, con la de 72 hembras presentes en un área de agricultura intensa con 9% de herbaceas en el Condado de Kossuth, Iowa. Fechas medias para el comienzo de la incubación de los primeros nidos fueron casi identicas en ambas áreas, pero las fechas medias de incubación para reanidajes fueron más tempranas en Palo Alto (22 de junio) que en Kossuth (5 de julio). El promedio de camada en los primeros nidos fue de 12.6 huevos, el cual fue mayor para la camada de 9.9 huevos en esfuerzos de reanidar. El éxito de los primeros nidos fue de 57.3% en Palo Alto y de 44.8% en Kossuth, mientras que el éxito de reanidajes fue de 45.6% en Palo Alto y solo de 26.9% en Kossuth. Regresiones lineares y logísticas revelaron que el éxito de anidaje promedió 62.3% en bloques de habitat no alterados tales como el CRP versus un 44.8% en habitats pequeños, lineares o alterados, independientes de el área de estudio. El éxito de las hembras promedió un 70.6% en Palo Alto y 52.2% en Kossuth, y varió más a través de los años en Kossuth. El éxito de anidaje en esta especie fue mayor en un espacio agrícola diversificado con grandes bloques de habitat no alterado. Cuando el anidaje se restringe a fragmentos de habitat pequeños o alterados la reproducción de la especie probablemente se reduce lo suficiente para limitar la tasa potencial de aumento poblacional.

Poor reproductive success and loss of nesting and brood habitat as a result of intensified agriculture was a major factor involved in observed declines in populations of Ring-necked Pheasants (*Phasianus colchicus*)

(Farris et al. 1977, Warner 1979, Warner et al. 1984, Etter et al. 1988) and other bird species (Rodenhouse et al. 1993, Herkert 1994, Warner 1994) throughout the Midwest. As land use changed, so did the relative influence of factors considered important to reproductive success, including the structure of vegetation in nesting habitat, the frequency of farming-related disturbances, the availability of blocks of grassland as compared to linear habitats, and local predator populations (Dumke and Pils 1973, Gates and Hale 1975, Warner et al. 1987, Warner 1988, Peterson et al. 1988). The logical response of wildlife managers to intensified agriculture was to conclude that establishing undisturbed nesting cover provided great opportunity for enhancing declining pheasant populations including along roadsides (Joselyn et al. 1968), or in warm season grass pastures (George et al. 1979, Warner et al. 1987). Despite efforts to manage more effectively the cover that remained, there was increasing evidence that fragments of quality habitat in a matrix of agricultural fields were not adequate to support large pheasant populations. With the establishment of the Conservation Reserve Program (CRP) in the late 1980s, biologists were hopeful that the large blocks of perennial grassland cover would substantially improve pheasant reproduction. Since CRP implementation, conditions for population growth and increased diversity have been improved for many species, including pheasants (Kimmel et al. 1992, Warner 1994, King and Savidge 1995, Riley 1995, Best et al. 1997). Avian ecologists and managers also began to recognize that population response was a function of not only the amount of habitat but also the configuration (Rodenhouse et al. 1993, Best et al. 1997). In 1989, we began a study to understand the role of landscape changes, particularly the establishment of CRP, on pheasant populations in northern Iowa, with the eventual goal of integrating all aspects of the life cycle into a stochastic population model. We have reported on winter survival of hens (Perkins et al. 1997) and survival of chicks during brood rearing (Riley et al. 1998) in previous papers. The specific objective of this paper is to report on nesting ecology of pheasants during a period after the establishment of CRP and to compare reproductive success between an intensively farmed landscape and a diverse landscape.

STUDY AREA

We conducted this study on two sites on the Des Moines Lobe glacial landform of north central Iowa (Prior 1991). We selected a 93.2 km² site dominated by intensive row crop agriculture on generally low relief glacial terrain in Kossuth County. The landscape is dominated by the squaremile road system, roughly evenly spaced farmsteads, and few large patches of hay-field or CRP land. Road ditches, waterways, and fencelines compose the majority of perennial-grass nesting habitat at the Kossuth area. Habitat composition in the Kossuth area was 86% row crops, 10% perennial grasses, 2% woody, and 2% other cover types. In contrast, the 124.3 km² area located in northwestern Palo Alto County and adjoining Clay County is on lateral moraine topography. The landscape at the Palo Alto area is less dominated by row crop fields than Kossuth, and also includes contiguous CRP fields, hay and pasture lands, and wetland and upland complexes managed for wildlife by public agencies. Numerous state-owned public areas and large blocks of set-aside lands provide abundant, undisturbed perennial grass nesting cover. Habitat composition in the Palo Alto area was 57% row crop, 25% grass, 6% wetland, 4% woody, and 8% other cover types. Perkins et al. (1997) provide maps and a detailed description of these study areas.

METHODS

Pheasant hens were captured each year from 1989–1994 by nightlighting in the fall (September–November), and by bait trapping when snow cover allowed (December–March) (Perkins et al. 1997). Hens were marked with leg bands and 12-g necklace-type radio transmitters (Riley and Fistler 1992) equipped with mortality switches (Holohill Systems, Ltd., Woodlawn, Ontario, Canada). We collected the proximal primary feather or measured the bursa of Fabricius (mm) (Wishart 1969) in order to age birds. Proximal primaries were dried and measured following Greenberg et al. (1972). Capturing and handling of birds were consistent with the AOU guidelines (American Ornithologists' Union 1988) and were approved by the Committee on Animal Care of Iowa State University.

We determined the date of mortality, causes of mortality, and reproductive success by monitoring radioed hens daily from 1 April through 15 August each year. When hens began localized daily movements with UTM coordinates within the average distance of the telemetry error polygon (White and Garrott 1990), we considered this to indicate settling and laying behavior (Riley et al. 1998). Hens that remained at the same UTM location for 3 d were assumed to be incubating. We visited a nest site only when telemetry indicated hens were away from nests after the hen was judged to have laid a complete clutch. We determined clutch size and candled the eggs to verify the date when incubation began (Fant 1957) and to predict date of hatching (Riley et al. 1998).

We adopted definitions and procedures developed by Corwardin et al. (1985) to analyze nesting data. We conservatively used initiation of incubation as evidence of a nesting attempt because we could not always find a nest during settling and laying. We considered a nest successful if ≥ 1 egg hatched. This approach has advantages over more traditional methods of searching cover for nests because the radioed hen is the sample unit. Difficulties encountered when estimating nest success from samples of clutches gathered by flushing hens (Klett et al. 1986), which require use of the Mayfield method (Mayfield 1961), are largely avoided with radio-marked birds. Partial clutch loss was determined by counting and examining all eggs on the date of hatch. We identified hatched eggs by the presence of detached shell membranes (Klett et al. 1986). Mortality of hens was directly observed from radio recoveries. We classified nest failures into mammalian, avian, and unknown predation, human disturbance including mowing, weather, and abandonment. Predator losses

were distinguished by examining field signs in the vicinity of the nest and at the site where transmitters were recovered (Perkins et al. 1997, Riley et al. 1998).

Hen success, the number of hens producing young divided by all hens in the sample (Cowardin et al. 1985, Klett et al. 1986, Vangilder and Kurzejeski 1995), was directly estimated from the radioed sample of birds. Destroyed and abandoned nests were treated similarly in calculating nest and hen success, unless we judged that observer disturbance was responsible for abandonment. Only hens remaining on the study areas and attempting to nest were included in calculations of hen and nest success. We continued to track intensively hens that resumed nest searching behavior so that we could distinguish failed initial nesting attempts from subsequent nesting attempts.

We defined nest cover by the dominant plant type within 1 m of the nest bowl. At the landscape scale, we distinguished three habitat types that we thought would be functionally different with regard to nesting. The first of these was square and rectangular blocks of grassland that were not disturbed during nesting, and included CRP, undisturbed oat fields, and wildlife management areas. Second, we grouped road right-of-ways, fencelines, waterways, and drainage ditches into linear habitat. A third habitat type was called other and included alfalfa fields, farmsteads, cemeteries, and non-farmed areas.

We used medians and 10 and 90% quantiles to describe and compare incubation dates between areas, years, age of the hen, nesting attempt, and nest outcome. We used general linear model procedures (SAS Institute, Inc. 1990) to analyze incubation dates and clutch size, using LSMEANS procedures to detect differences following an F-test. For nest and hen success rates, we used a ratio estimator to calculate an overall rate estimate among years (r = number of hens successful in year $i \div$ number of hens attempting to nest in year *i*, summed over years) and their associated standard errors (Cochran 1963:157-158). We modeled nest and hen success, and nest mortality factors as functions of areas, years, ages, nest attempts, cover at the nest, and habitat type surrounding the nest using linear logistic regression (PROC LOGISITIC, SAS Institute, Inc. 1990). Our study is observational (Eberhardt and Thomas 1991) and we focused on estimation and testing of parameters, model revision and variable selection, and goodness of fit of the models. As such, our inferential statements apply to characteristics of the models and the implications for the real world (Hilborn and Mangel 1997).

RESULTS

Nesting chronology and clutch size.—We collected information on 245 radioed hen pheasants between 1990–1994. These hens initiated 288 nests and hatched eggs in 142 nests. Median incubation date of first nest attempts at Kossuth was 23 May versus 24 May at Palo Alto, averaged over all years. Median incubation date of subsequent renesting attempts at Kossuth was 5 July, whereas it was 22 June at Palo Alto (Table 1). Median

	Nest attempt								
-			Initial				Renest		
Year/study area	n	10% quantile	Incubation date	90% quantile	n	10% quantile	Incubation date	90% quantile	
1990									
Palo Alto Kossuth	19 8	5 May 25 Apr	20 May 27 May	28 May 16 Jul	8 4	30 May 19 Jun	14 Jun 30 Jun	28 Jun 14 Jul	
1991									
Palo Alto Kossuth	18 6	16 May 13 May	29 May 27 May	5 Jun 10 Jun	2 6	27 May 11 Jun	3 Jun 30 Jun	10 Jun 27 Jul	
1992									
Palo Alto Kossuth	$\frac{43}{8}$	10 May 7 May	24 May 20 May	12 Jun 28 Jun	$12 \\ 4$	9 Jun 9 Jun	26 Jun 17 Jul	4 Aug 29 Jul	
1993									
Palo Alto Kossuth	29 11	5 May 9 May	25 May 14 May	11 Jun 28 May	22 3	6 Jun 1 Jul	23 Jun 1 Jul	12 Jul 2 Aug	
1994									
Palo Alto Kossuth	23 20	6 May 4 May	23 May 23 May	10 Jun 5 Jun	9 2	2 Jun 1 Jul	28 Jun 3 Jul	1 Aug 5 Jul	
1990-1994									
Palo Alto Kossuth	132 53	7 May 7 May	24 May 23 May	10 Jun 10 Jun	$53 \\ 19$	2 Jun 11 Jun	22 Jun 5 Jul	14 Jul 29 Jul	

TABLE 1. Median date and range between 10% and 90% quantiles of initiation of incubation for radioed female Ring-necked Pheasants in Palo Alto and Kossuth counties, Iowa, 1990–1994.

incubation dates did not differ between ages ($F_{1,185} = 0.34$, P = 0.563) nor successful and unsuccessful nests ($F_{1,223} = 0.16$, P = 0.692), so we pooled data by age and nest fate. The pooled analysis of variance showed a significant study area by nest attempt interaction ($F_{1,237} = 9.56$, P =0.002). Median incubation dates for second and third nests were consistently later at Kossuth versus Palo Alto (P = 0.001). Median incubation dates for first nests did not differ between the two areas (P = 0.974).

When data from both areas were combined, average clutch size of first nests was 12.6 eggs but averaged only 9.9 eggs in renesting attempts. There were no differences in clutch size between ages ($F_{1,101} = 0.04$, P = 0.849). Again we pooled the ages, and clutch size of successful nests did not differ between study areas ($F_{1,119} = 0.22$, P = 0.929) nor among years ($F_{1,119} = 0.33$, P = 0.569). Clutches in first nests were larger than renests ($F_{1,119} = 6.58$, P = 0.012) (Table 2). Clutch size declined at a rate of 0.08 eggs/day as a function of initiation date ($F_{1,128} = 104.30$, $P \le 0.001$, $r^2 = 0.45$, Fig. 1).

The histogram of dates of all nest initiations differed between Palo Alto and Kossuth (Fig. 2). More nests were initiated at Palo Alto and the median of the nesting distribution (29 May) was close to the mean (2 June),

			Nest a	ttempt		
- Year/study		First nest			Renest	
area	n	x	SE	n	x	SE
1990						
Palo Alto Kossuth	$\frac{13}{8}$	$\begin{array}{c} 12.2 \\ 12.1 \end{array}$	$\begin{array}{c} 0.62 \\ 1.09 \end{array}$	4 4	$\begin{array}{c} 10.5 \\ 10.8 \end{array}$	$0.87 \\ 0.95$
1991						
Palo Alto Kossuth	18 1	$\begin{array}{c} 12.4 \\ 13.0 \end{array}$	0.47	2 1	$\begin{array}{c} 13.0\\ 8.0\end{array}$	2.00
1992						
Palo Alto Kossuth	27 4	13.1 12.0	$\begin{array}{c} 0.65\\ 0.41\end{array}$	6 2	$\begin{array}{c} 10.0\\ 11.0 \end{array}$	$\begin{array}{c} 1.15 \\ 2.00 \end{array}$
1993						
Palo Alto Kossuth	9 4	$11.9 \\ 15.3$	$0.84 \\ 0.25$	10 0	9.0	0.75
1994						
Palo Alto Kossuth	$\frac{10}{12}$	$\begin{array}{c} 10.5 \\ 14.1 \end{array}$	$\begin{array}{c} 1.20 \\ 0.70 \end{array}$	$2 \\ 0$	8.5	2.50
1990–1994						
Palo Alto Kossuth	77 29	12.3 13.4	$\begin{array}{c} 0.34 \\ 0.52 \end{array}$	24 7	9.8 10.4	$\begin{array}{c} 0.46 \\ 0.78 \end{array}$

 TABLE 2.
 Mean clutch size of successful nests of radioed female Ring-necked Pheasants in Palo Alto and Kossuth counties, Iowa, 1990–1994.

with a single peak (kurtosis = 0.678). At Kossuth the median initiation date (28 May) was also close to the mean (3 June), but the frequency histogram was more flat-topped (kurtosis = -0.419), indicating that nest initiation was more protracted because of late renesting.

Nest success.—Preliminary analysis showed that fewer nests were initiated and nest success was lower in 1993 on both study areas than in all other years except 1994. But, because of the low sample size in 1993, we did not consider specific year effects in our logistic regression model. Percent success of first nests pooled over all years was 57.3% at Palo Alto and 44.8% at Kossuth, whereas success of subsequent renests was 45.6% at Palo Alto but only 26.9% at Kossuth (Table 3). Overall success at Palo Alto was 53.8% versus 39.8% at Kossuth. When we used linear logistic regression to model nest success, preliminary analyses showed that nests in linear and other habitats had lower success than nests in block habitats. In subsequent analyses, we combined linear and other into a habitat type that we visualized as small or disturbed habitat fragments and compared these with large undisturbed blocks. When we fit the overall model with area, age, nest attempt, nest cover, and block versus linear habitat type, we rejected the global null hypothesis that all covariates were zero (χ^2 = 13.29, df = 5, P = 0.021). Coefficients for study area ($\chi^2 = 0.583$, df =



FIGURE 1. Relationship of clutch size to date of nest initiation, areas and years combined, for radioed female Ring-necked Pheasants in Palo Alto and Kossuth counties, Iowa, 1990–1994.



FIGURE 2. Dates of nest initiation for successful nests, years combined, of radioed female Ring-necked Pheasants in Palo Alto and Kossuth counties, Iowa, 1990–1994.

	First nest		Renest		Combined	
Year/study area	n	%	n	%	n	%
1990			-			
Palo Alto	23	56.5	11	45.5	34	52.9
Kossuth	17	47.1	8	50.0	25	48.0
1991						
Palo Alto	20	90.0	2	100.0	22	90.9
Kossuth	10	20.0	9	11.1	19	15.8
1992						
Palo Alto ^b	43	62.8	13	46.2	56	58.9
Kossuth	8	50.0	4	50.0	12	50.0
1993						
Palo Alto	29	34.5	22	45.5	51	39.2
Kossuth	11	36.4	3	0.0	14	28.6
1994						
Palo Alto	23	47.8	9	33.3	32	43.8
Kossuth	21	57.1	2	0.0	23	52.2
1990-1994						
Palo Alto ^c	138	57.2 ± 8.0	57	45.6 ± 3.0	195	53.8 ± 6.8
Kossuth	67	44.8 ± 6.3	26	26.9 ± 11.6	93	39.8 ± 7.3

TABLE 3.	Number of nests ^a	and success rate	of radioed	female	pheasants	in Palo Alto and
Kossu	th counties, Iowa,	1990-1994.			-	

^a Does not include observer-caused abandonment, nests where fate was unknown, or hens that nested off study areas.

 $^{\rm b}$ Includes one hen that hatched a nest, lost the brood, and successfully renested. c \bar{x} \pm SE.

1, P = 0.445), age ($\chi^2 = 0.883$, df = 1, P = 0.347), nest attempt ($\chi^2 = 0.331$, df = 1, P = 0.565), and nest cover ($\chi^2 = 3.151$, df = 1, P = 0.076) were not different from zero. However, habitat type was different from zero ($\chi^2 = 5.398$, df = 1, P = 0.02). Using stepwise selection to assess variables, a model with only an intercept and habitat type fit the data as well as the global model ($\chi^2 = 4.78$, df = 4, P = 0.310). Based on this model in which data are pooled with regard to year and area, nest success averaged 62.3% in undisturbed block habitats versus 44.8% in small or disturbed habitat fragments.

Hen success.—Hen success averaged 70.6% at Palo Alto and 52.2% at Kossuth during the years 1990–1994. Hen success was more variable among years at Kossuth than at Palo Alto (Table 4). When we fit a logistic regression model of hen success as a function of area, year, and age, we failed to reject the global null hypothesis that all covariates were equal to zero ($\chi^2 = 11.06$, df = 6, P = 0.087). However, the coefficient for area was significantly different from zero ($\chi^2 = 4.803$, df = 1, P = 0.028).

Nest fate.—The major cause of nest failure was predation (73.6%, n = 69 nests with known fate). We confirmed 24.6% losses from mammalian

Year/study area	<i>n</i>	Hen success (%)
lear/study area	n	(70)
1990		
Palo Alto	28	64.3
Kossuth	18	66.7
1991		
Palo Alto	22	90.9
Kossuth	11	27.3
1992		
Palo Alto	44	72.7
Kossuth	8	62.5
1993		
Palo Alto	29	69.0
Kossuth	11	36.4
1994		
Palo Alto	23	56.5
Kossuth	21	57.1
1990-1994		
Palo Alto ^b	146	70.5 ± 4.5
Kossuth	69	52.2 ± 7.1

TABLE 4. Number^a and proportion of radioed female pheasants successful in one or more nest attempts in Palo Alto and Kossuth counties, Iowa, 1990–1994.

^a Does not include observer caused abandonment, nests where fate was unknown, or hens that nested off study areas.

 ${}^{\mathrm{b}}\bar{\mathrm{x}} \pm \mathrm{SE}.$

predation (n = 17) and 4.3% from avian predation (n = 3), with a large proportion where we could not distinguish the two types of predation losses (n = 31). The remaining losses (26.4%) included those caused by farm operations, weather, and abandonment. When we modeled predation versus other losses we rejected the global null hypothesis that coefficients for area, age, nest attempt, nest cover, and habitat type were all equal to zero ($\chi^2 = 7.71$, df = 5, P = 0.003). Because of small sample size of confirmed losses we could only reasonably make inferences about area effects, which showed that predation caused significantly more nest failures in Palo Alto than in Kossuth ($\chi^2 = 8.06$, df = 1, P = 0.005). At Palo Alto 87.5% of all failures were caused by predators, whereas at Kossuth this percentage was only 42.9% and disturbance and weather were correspondingly more important.

DISCUSSION

Landscape characteristics had an important influence on nesting chronology. Pheasants initiated nesting at similar times on both areas, but subsequent renesting attempts were substantially later at the fragmented landscape of Kossuth. The delay has a cascading effect on production because clutch sizes declined throughout the season because physiological condition changes (Labisky and Jackson 1969, Riley et al. 1994, Niewoonder et al. 1998). Furthermore, nesting was more protracted at Kossuth because a relatively larger proportion of nests are destroyed and renesting interval is relatively fixed behaviorally (Dumke and Pils 1979). In total, a larger proportion of recruitment of chicks at Kossuth comes from renesting attempts later in the season. Because Riley et al. (1998) showed that chick mortality rate increased by 2.3% for each day later in the season that they were hatched, later hatching has an important effect on recruitment of hens.

Nest success during renesting averaged only 27% at Kossuth, which accounts for most of the difference in the overall success rate differences of 54% at Palo Alto versus 40% at Kossuth. The explanation for this difference is that nesting cover in the Palo Alto landscape is arranged in large continuous blocks whereas at Kossuth nesting cover is configured in smaller linear fragments. Nest success was 40% higher in blocks of undisturbed cover compared with linear or small disturbed fragments of habitat. Other research has also reported higher nest success in large undisturbed blocks verses small linear or disturbed habitats (Warner et al. 1984, Riley et al. 1994). It is presumed that linear habitats such as road right-of-ways and fencelines serve as travel lanes for predators, and high rates of nest destruction have been observed therein (Gates and Hale 1975, Warner et al. 1987, Riley et al. 1994). However, Warner et al. (1987) point out that nest success in havfields in Illinois (25%) did not exceed success rate in seeded roadside tracts (29%), and that nest success in block cover may decline substantially over time. Even under the best conditions, nesting success in pheasant populations can be quite variable (Warner et al. 1987, Riley et al. 1994, Niewoonder et al. 1998) but a nest success of 46% is considered average (Hill and Robertson 1988).

Unlike nest success, estimated hen success was different between areas, indicating that the landscape context influences this parameter in some way. Our observation was that hens often moved, sometimes great distances, after a nest failed, so hen success is potentially influenced by both the initial nest success rate and renesting opportunity. A larger proportion of both initial and subsequent nesting attempts of hens at Kossuth are in small fragments of habitat with lower nest success, and consequently hen success was more variable among years at Kossuth. Our estimates of hen success for the two areas are very consistent with reports of 40 to 80% hen success (Gates and Hale 1975, Dumke and Pils 1979, Riley et al. 1994, Leif 1995).

A larger proportion of all nest failures at Palo Alto were caused by predators, whereas disturbance from farm operations and abandonment may be more important in fragmented landscapes like Kossuth. It is plausible that predator populations might have increased along with other wildlife populations in landscapes where many blocks of CRP habitat have been restored. We only have observations of dens, tracks, and other predator sign which indicate that predators, especially red fox (*Vulpes vulpes*), were more abundant at Palo Alto. Our observation of a greater proportion of nest destruction by predators at Palo Alto would be consistent with the idea that predators were more abundant there. Paradoxically, Warner et al. (1987) suggested that one consequence of limited habitat was that predator populations may also be low, resulting in equivalent nest success rates in linear habitats when compared to block habitats.

This study reaffirms the importance of a diversified agricultural landscape with large blocks of undisturbed habitat to pheasant reproduction. With greater predominance of large blocks of cover in the Palo Alto landscape, hens had a greater likelihood of selecting a habitat type which enhanced the probability of success. At Kossuth, nests in large blocks were still successful, but alternatives in the landscape were limited primarily to small or disturbed habitat fragments. Nesting success at Kossuth was below that considered average for the species, and renesting success was very low in most years. Populations cannot increase rapidly in landscapes dominated by small, linear or disturbed fragments of grassland because of the repeated failures of nests and hens. Low hen success combined with low survival of late-hatched chicks (Riley et al. 1998), results in populations that cannot sustain rates of recruitment that will yield an increase in standing densities (Hill and Robertson 1988). If current agricultural policy resulted in large blocks of secure nesting cover that were rotated throughout the landscape, the effects of predation on nesting pheasants might be reduced to the greatest degree. In prior decades, a diversified agriculture with small grains, hay, pasture, and odd areas that were constantly rotated provided the landscape management that wildlife professionals are challenged to recreate today.

ACKNOWLEDGMENTS

This study was supported by the Iowa Department of Natural Resources Project W-115-R, by cooperation with the Iowa Cooperative Fish and Wildlife Research Unit and the Department of Animal Ecology at Iowa State University. Pheasants Forever provided in-kind support. T. Z. Riley and P. A. Vohs developed initial phases of the project and we thank R. M. Barta, W. H. Bünger, T. H. Burger, M. R. Delay, M. E. Esty, D. E. Ewing, B. A. Fistler, A. W. Hancock, B. L. Hellyer, D. D. Hoffman, R. J. Munkel, D. M. Nelson, A. L. Perkins, and P. E. Reynolds for collecting field data. T. R. Bishop and B. J. Giesler manipulated the GIS data. This is Journal Paper J-17761 of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa; Projects 2401 and 3299.

LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1988. Report of committee on use of wild birds in research. Auk 105(1, Suppl.):1–41.

BEST, L. B., H. CAMPA III, K. E. KEMP, R. J. ROBEL, M. R. RYAN, J. A. SAVIDGE, H. P. WEEKS JR., AND S. R. WINTERSTEIN. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. Wildl. Soc. Bull. 25:864–877.

COCHRAN, W. G. 1963. Sampling techniques. 2nd ed. John Wiley and Sons, New York. 413 pp.

COWARDIN, L. M., D. S. GILMER, AND C. W. SHAIFFER. 1985. Mallard recruitment in the agricultural environment of North Dakota. Wildl. Monogr. 92. 37 pp.

DUMKE, R. T., AND C. M. PILS. 1973. Mortality of radio-tagged pheasants on the Waterloo Wildlife Area. Wisc. Dept. Nat. Resour. Tech. Bull. No. 72. 52 pp. ——, AND ———. 1979. Renesting and dynamics of nest site selection by Wisconsin pheasants. J. Wildl. Manage. 43:705–716.

- EBERHARDT, L. L., AND J. M. THOMAS. 1991. Designing environmental field studies. Ecol. Monogr. 61:53-73.
- ETTER, S. L., R. E. WARNER, G. B. JOSELYN, AND J. E. WARNOCK. 1988. The dynamics of pheasant abundance during the transition of intensive row-cropping in Illinois. Pp. 111– 127, in D. L. Hallett, W. R. Edwards, and G. V. Burger, eds. Pheasants: symptoms of wildlife problems on agricultural lands. North Central Sec., The Wildl. Soc., Bloomington, Indiana.
- FANT, R. J. 1957. Criteria for aging pheasant embryos. J. Wildl. Manage. 21:324-328.
- FARRIS, A. L., E. D. KLONGLAN, AND R. C. NOMSEN. 1977. The ring-necked pheasant in Iowa. Iowa Conservation Commission, Des Moines, Iowa. 147 pp.
- GATES, J. M., AND J. B. HALE. 1975. Reproduction of an east central Wisconsin pheasant population. Wisc. Dept. of Nat. Resour. Tech. Bull. 85. 70 pp.
- GEORGE, R. R., A. L. FARRIS, C. C. SCHWARTZ, D. D. HUMBURG, AND J. C. COFFEY. 1979. Native prairie grass pastures as nest cover for upland birds. Wildl. Soc. Bull. 7:4–8.
- GREENBERG, R. E., S. L. ETTER, AND W. L. ANDERSON. 1972. Evaluation of proximal primary feather criteria for aging wild pheasants. J. Wildl. Manage. 36:700–705.
- HERKERT, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecol. Appl. 4:461–471.
- HILBORN, R., AND M. MANGEL. 1997. The ecological detective: confronting models with data. Princeton Univ. Press, Princeton, New Jersey. 315 pp.
- HILL, D. A., AND P. A. ROBERTSON. 1988. A population model as an aid to pheasant management. Pp. 149–163, in D. L. Hallett, W. R. Edwards, and G. V. Burger, eds. Pheasants: symptoms of wildlife problems on agricultural lands. North Central Sec., The Wildl. Soc., Bloomington, Indiana.
- JOSELYN, G. B., J. E. WARNOCK, AND S. L. ETTER. 1968. Manipulation of roadside cover for nesting pheasants—a preliminary report. J. Wildl. Manage. 32:217–233.
- KIMMEL, R. O., A. H. BERNER, R. J. WELSH, B. S. HAROLDSON, AND S. B. MALCHOW. 1992. Population responses of grey partridge (*Perdix perdix*), ring-necked pheasants (*Phasia-nus colchicus*), and meadowlarks (*Sturnella* sp.) to farm programs in Minnesota. Pp. 797–806, *in* M. Birkan, ed. Proceedings of Perdix IV. First international symposium on partridges, quails, and francolins. Gibier Faune Sauvage 9.
- KING, J. W., AND J. A. SAVIDGE. 1995. Effects of Conservation Reserve Program on wildlife in southeast Nebraska. Wildl. Soc. Bull. 23:377–385.
- KLETT, A. T., H. F. DUEBBERT, C. A. FAANES, AND K. F. HIGGINS. 1986. Techniques for studying nest success of ducks in upland habitats in the Prairie Pothole region. U.S. Fish and Wildl. Serv. Resour. Publ. 158. 24 pp.
- LABISKY, R. F., AND G. L. JACKSON. 1969. Production and weight of eggs laid by yearlings, 2and 3-year-old pheasants. J. Wildl. Manage. 33:718–721.
- LEIF, A. P. 1995. Survival and reproduction of wild and pen reared ring-necked pheasant hens. J. Wildl. Manage. 58:501–506.
- MAYFIELD, H. 1961. Nesting success calculated from exposure. Wilson Bull. 73:255–261.
- NIEWOONDER, J. A., H. H. PRINCE, AND D. R. LUUKKONEN. 1998. Survival and reproduction of female Sichuan, ring-necked, and F₁ hybrid pheasants. J. Wildl. Manage. 62:933–938.
- PERKINS, A. L., W. R. CLARK, T. Z. RILEY, AND P. A. VOHS. 1997. Effects of landscape and weather on winter survival of ring-necked pheasant hens. J. Wildl. Manage. 61:634–644.
- PETERSON, L. R., R. T. DUMKE, AND J. M. GATES. 1988. Pheasant survival and the role of predation. Pp. 166–196, in D. L. Hallett, W. R. Edwards, and G. V. Burger, eds. Pheasants: symptoms of wildlife problems on agricultural lands. North Central Sec., The Wildl. Soc., Bloomington, Indiana.
- PRIOR, J. C. 1991. Landforms of Iowa. Univ. of Iowa Press, Iowa City, Iowa. 153 pp.
- RILEY, T. Z. 1995. Association of the Conservation Reserve Program with ring-necked pheasant survey counts in Iowa. Wildl. Soc. Bull. 23:386–390.
 - —, AND B. A. FISTLER. 1992. Necklace radio transmitter attachment for pheasants. J. Iowa Acad. Sci. 99:65–66.

—, J. B. WOOLEY, AND W. B. RYBARCZYK. 1994. Reproduction of ring-necked pheasants in Iowa. Prairie Nat. 26:263–272.

-----, W. R. CLARK, D. E. EWING, AND P. A. VOHS. 1998. Survival of ring-necked pheasant chicks during brood rearing. J. Wildl. Manage. 62:36–44.

- RODENHOUSE, N. L., L. B. BEST, R. J. O'CONNOR, AND E. K. BOLLINGER. 1993. Effects of temperate agriculture on Neotropical landbirds. Pp. 280–295, in D. M. Finch and P. M. Stangel, eds. Status and management of Neotropical migratory birds. U.S. Dept. Agr. For. Serv. Gen. Tech. Rep. RM-229.
- SAS INSTITUTE INC. 1990. SAS/STAT User's guide. Version 6. 4th ed. SAS Inst. Inc., Cary, North Carolina. 1686 pp.
- VANGILDER, L. D., AND E. W. KURZEJESKI. 1995. Population ecology of the eastern wild turkey in northern Missouri. Wildl. Monogr. 130. 50 pp.
- WARNER, R. E. 1979. Use of cover by pheasant broods in east-central Illinois. J. Wildl. Manage. 43:334-346.
 - 1988. Habitat management: how well do we recognize the pheasant facts of life? Pp. 129–146, *in* D. L. Hallett, W. R. Edwards, and G. V. Burger, eds. Pheasants: symptoms of wildlife problems on agricultural lands. North Central Sec., The Wildl. Soc., Bloomington, Indiana.

——. 1994. Agricultural land use and grassland habitat in Illinois: future shock for Midwestern birds. Conserv. Biol. 8:147–156.

-, G. B. JOSELYN, AND S. L. ETTER. 1987. Factors affecting roadside nesting by pheasants in Illinois. Wildl. Soc. Bull. 15:221–228.
- WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-racking data. Academic Press, San Diego, California. 383 pp.
- WISHART, W. 1969. Age determination of pheasants by measurement of proximal primaries. J. Wildl. Manage. 33:714–717.

Received 16 Feb. 1998; accepted 9 Oct. 1998.