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DOES MALLARD CLUTCH SIZE VARY WITH LANDSCAPE COMPOSITION: A DIFFERENT VIEW

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ABSTRACT.—We report on the relationship between Mallard (*Anas platyrhynchos*) clutch size and cropland area in the landscape in western Minnesota during 1997–1999. We measured clutch size in two types of nest structures and fit a mixed-effects model to the data to examine the relationship. Our model also included covariates to control for the effects of year, nest initiation date, estimated pair numbers, and nest structure type. Unique landscapes associated with each nest (n = 134) ranged from 46.4–84.8% cropland. Clutch size was unrelated to cropland area, nest structure type, and estimated number of pairs with access to structures. Mean clutch size declined with nest initiation date early in the nesting season, but increased somewhat for nests initiated after 30 May. Clutch size also differed among years. Mean clutch size, adjusted for nest initiation date, was 11.0 ± 0.19 SE for 1997, 10.5 ± 0.19 SE for 1998, and 11.0 ± 0.19 SE for 1999. Conclusions regarding the significance of the year effect and the degree of nonlinearity due to nest initiation date were sensitive to potential clutch size outliers, but cropland area had no effect on clutch size regardless of the way we constrained clutch size. Nest parasitism by philopatric females laying in certain structures might explain the observed increase in clutch size in late nest initiations. *Received 29 June 2003, accepted 24 August 2003.*

Population size and the recruitment of young in Mallards (*Anas platyrhynchos*) are related to many factors in the landscape. Krapu et al. (1997) observed a negative relationship between the abundance of Mallard pairs and the amount of cropland in a landscape. Further, Greenwood et al. (1995) and Reynolds et al. (2001) have reported that nest success was greater in landscapes where the proportion of cropland was lower compared to that observed in landscapes with more cropland. Ball et al. (2002) recently examined the relationship between Mallard clutch size and landscape composition in North Dakota, concluding that clutches in landscapes having little cropland were larger than those in landscapes having more cropland. Their results suggest yet another way recruitment might be affected by land use. Their data came from a study of elevated nest structures that was designed to assess the influence of landscapes on Mallard use of nest structures (Artmann et al. 2001). A relationship between clutch size and landscape composition had not previously been reported for waterfowl. Thus, their results were novel and they encouraged researchers to examine the relationship in other locations and for other species of waterfowl. We initiated a study in Minnesota in 1996 that had similar objectives to those of Artmann et al. (2001). Here we report on the relationship between cropland area and Mallard clutch sizes that we observed in our study after we controlled for the effects of date of nest initiation, Mallard abundance, and nest structure type.

STUDY AREA AND METHODS

Our study area included 658 km^2 in southern Grant and northern Stevens counties (45° 51′ N, 96° 02′ W), Minnesota. The area is intensively cultivated and upland nesting cover for Mallards was restricted primarily to scattered tracts of mixed native and exotic grasses and forbs on state and federally managed wildlife areas, grassy fields in agricultural set-aside programs, and cover in roadside right-of-ways. Wetland drainage also has been extensive through the use of surface ditches and subsurface drainage tiles (Prince 1997). Most remaining wetlands have permanent or semipermanent water regimes due to the consolidation of temporary and seasonal wetlands into deeper, more permanent basins. Mean Mallard breeding pair density was about 4 pairs/km^2 (R. Johnson unpubl. data).

We used aerial photos to select wetlands throughout the study area that were candidates for nest structure placement. We subjectively

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assessed whether a wetland had much, a moderate amount, or little cropland within about 1 km. We then selected approximately equal numbers of wetlands from each cropland class for nest structure placement. We used this strategy to assure that structures with much or little surrounding cropland would be well represented in our sample. During spring 1996, one structure was placed in each of 78 wetlands while two structures were placed in each of 16 of the largest wetlands for a total of 110 structures. Nest structure type, either a single or double nest cylinder, was assigned randomly each time a structure was erected. We inspected each structure four times each year to record nesting attempts.

We built a geographic information system (GIS) describing the land use on the study area during 1997–1999, and we used the GIS to describe landscape composition around each nesting structure within a circular area having a 3.2-km radius from the structure. This distance approximates the distance hen Mallards will travel to nesting cover (Reynolds et al. 1996). The landscape composition within each circular area described the "landscape" (32.2 km^2) surrounding each clutch. The number of Mallard pairs with access to each nest structure also was modeled with a GIS (Reynolds et al. 1996, R. Johnson unpubl. data).

We fit a mixed-effects model (PROC MIXED; SAS Institute, Inc. 2000) to test for a relationship between landscape composition and clutch size in nest structures. Fixed effects included the amount of cropland in the landscape as well as covariates for year, nest initiation date, pair numbers, and deployment type (one versus two cylinders). We included covariates for year and nest initiation date because clutch size in waterfowl can vary among years and within season (Alisauskas and Ankney 1992, Rohwer 1992). We also included covariates for pair numbers and nest structure type because nest parasitism occurred in our nest structures (Zicus et al. 2003) and the influence of different structure types was unknown.

Exploratory plots suggested a nonlinear relationship between clutch size and nest initiation date. Quadratic and cubic date effects were included in the model using orthogonal polynomials to avoid problems of collinearity (PROC IML; SAS Institute, Inc. 1989). We also centered both pair numbers and amount of cropland in the landscape (by subtracting their means from all observations) to avoid collinearity (Kleinbaum et al. 1988:208). A random subject effect (corresponding to each unique structure) was included to account for possible nonindependence among clutch sizes observed in the same structure within and among years. We used normal probability plots to validate normality assumptions of the random effect and of the within group errors (Pinheiro and Bates 2000). We assessed homogeneity of variance of the within group errors using plots of residuals versus fitted values. We tested significance of fixed effects parameters using F statistics with denominator degrees of freedom calculated using the KR method (Schaalje et al. 2002).

Clutches as large as 25 occurred in the nests that we monitored. Inspection of the distribution of observed clutch sizes suggested clutches >16 were statistical outliers. Consequently, we fit the model to clutch sizes of <17 and conducted a sensitivity analysis to assess robustness of the conclusions with respect to data sets within which clutch size was variously constrained. We also assessed robustness by fitting the model both with and without the random effect and used Akaike's Information Criterion (AIC) values to choose among competing models. The AIC value for the mixed effects model was smaller, suggesting a better fit to the data.

RESULTS

We determined clutch size for 139 nests from 1997–1999. Four clutches in single cylinder structures and one in a double cylinder structure contained >16 eggs and thus were censored from the data. Landscapes associated with each clutch varied in the percent cropland (Fig. 1) with a median of 66.1% (mean = 65.8%, range = 46.4–84.8%). We detected no relationship between clutch size and cropland area ($F_{1,55.5} = 0.10$, $P = 0.76$), structure type ($F_{1,46.1} = 0.0$, $P > 0.99$), or the number of pairs with access to a structure ($F_{1,47.5} = 0.02$, $P = 0.88$). However, nest initiation date was related to clutch size (linear date, $F_{1,123} = 65.5$, $P < 0.0001$; quadratic date, $F_{1,129} = 21.2$, $P < 0.0001$; cubic date, $F_{1,122} = 3.9$, $P = 0.051$) in a curvilinear way (Fig. 2), and

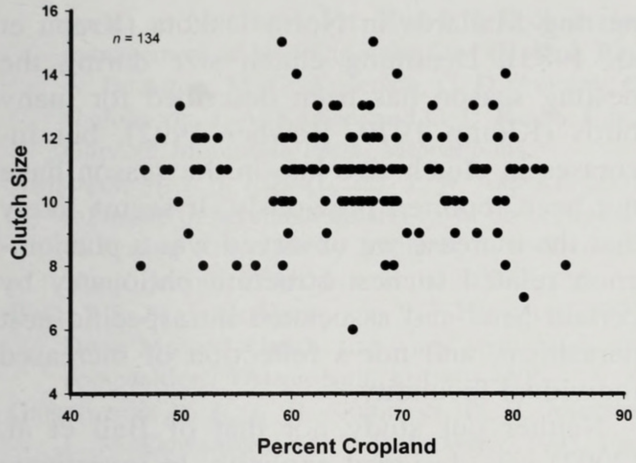

FIG. 1. There was no apparent relationship between Mallard clutch size in nest structures and percent cropland in 134 western Minnesota landscapes that were each 32.2 km² in size, 1997–1999.

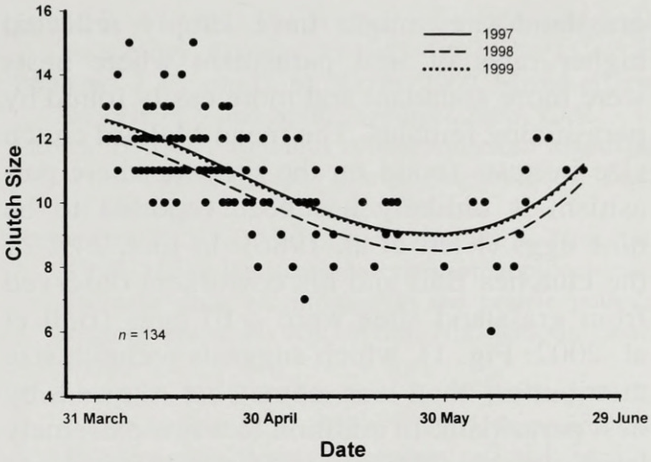

FIG. 2. Mallard clutch size in nest structures was modeled as having a curvilinear relationship to nest initiation date in western Minnesota, 1997–1999.

year had a marginally significant effect on clutch size ($F_{2,101}$ = 2.8, P = 0.065). Mean clutch size, adjusted for nest initiation date, was 11.0 ± 0.19 SE for 1997, 10.5 ± 0.19 SE for 1998, and 11.0 ± 0.19 SE for 1999. Cropland area was not a significant predictor of clutch size regardless how we constrained clutch size in the analysis.

DISCUSSION

We detected no relationship between Mallard clutch size and landscape composition, in contrast to the findings of Ball et al. (2002). However, our study differed in several aspects from that of Ball and his coworkers. First, Mallard pair density in our study was only 30–40% of that in the North Dakota study and our nest structure density was about 10% of theirs (Ball et al. 2002). Perhaps more importantly, we defined landscapes differently. The landscape associated with each clutch in our sample was unique, extending for 3.2 km (32.2 km²) around each nest location and was intended to approximate the distance a Mallard hen would travel to nesting cover (Reynolds et al. 1996).

In contrast, Ball and his coworkers delineated 13 smaller (10.4-km²) study sites and identified them as cropland (mean = 68.9% cropland) or grassland (mean = 30.2% cropland) and classified clutches as being from either a cropland or grassland landscape. Likely, the home range of all hens would not have been entirely within their study sites, nor is it known how far individual hens traveled to reach the nest structures in the North Dakota study. Presumably, landscape composition surrounding their study sites was similar to that within each site, and thus classification of a clutch based on the amount of cropland in the entire home range of a hen would not have changed.

Further, ours was a multiyear study in which we analyzed clutch size using regression allowing the amount of cropland in the landscape associated with a clutch to vary continuously. We also included covariates for date of nest initiation, nest structure type, and estimated number of Mallard pairs with access to the nest structure to control for the effects these variables might have on clutch size. In comparison, Ball and his coworkers analyzed data from a single year comparing cropland and grassland landscapes using analysis of covariance that controlled for the effect of date of nest initiation.

We observed a few very large clutches in our data that were statistical outliers. However, we detected no relationship between clutch size and amount of cropland in the surrounding landscape regardless of how we constrained clutch size in our analysis. We suspect that the novel relationship between clutch size and landscape composition reported by Ball and his coworkers might have been an artifact of their data. Sample sizes in the North Dakota study were relatively small with only seven clutches measured from six cropland study sites and 34 nests from seven grassland sites.

As they acknowledged, larger clutches from grassland sites might have simply reflected higher rates of nest parasitism where nests were more abundant and more easily found by parasitizing females. The mean Mallard clutch size in nests found on the ground where parasitism is unlikely has been reported to be nine eggs (Klett et al. 1986). In fact, 24% of the clutches Ball and his coworkers observed from grassland sites were >10 eggs (Ball et al. 2002: Fig. 1), which suggests a clutch size distribution that was somewhat skewed by nest parasitism. In addition to a few extremely large clutches, the pattern of parasitism in our sample seemed to be reflected by a higher frequency of 10- to 12-egg clutches over what might be expected in the absence of parasitism. Although they observed no clutches >10 eggs from their sites with abundant cropland, their sample of seven clutches was likely insufficient to truly represent the underlying clutch size distribution for structure nests in this type of landscape.

We attempted to control for parasitism in our model by including a covariate for the number of Mallard pairs having access to nest structures, but estimated pair numbers were unrelated to clutch size. This lack of association might have resulted from the fact that the pair values we relied on were estimated using a GIS model (Reynolds et al. 1996). As such, the estimates might not reflect actual pair numbers. Alternatively, conditions other than mallard abundance might influence intraspecific parasitism of Mallard nest structures and might explain our failure to detect a pair-number effect on clutch size that was separate from the cropland effect.

We observed a tendency for nests in certain nest structures to be parasitized more than others. This complicated clutch size modeling, but might explain the nonlinear trend in clutch sizes with respect to nest initiation date. For example, three of four clutches >20 eggs occurred in the same nest structure. Also, many nests initiated after 30 May were in the same nest structures that had large clutches earlier in the nesting season. Perhaps, something about these specific structures predisposed them to nest parasitism. When nests initiated after 30 May were ignored, clutch size declined at a similar rate (0.066 eggs/day) as that (0.064 eggs/day) reported by Ball et al. (2002) and that (0.054 eggs/day) observed for ground nesting Mallards in North Dakota (Krapu et al. 1983). Declining clutch size during the nesting season has been described for many birds (Klomp 1970, Rowher 1992), but increases in clutch size late in the season have not been reported previously. It seems likely that the increase we observed was a phenomenon related to nest structure philopatry by certain hens and associated intraspecific nest parasitism, and not a reflection of increased individual fecundity.

Neither our study nor that of Ball et al. (2002) was designed explicitly to investigate the influence of landscapes on clutch size, so both had limitations. Single-year studies with small sample sizes (i.e., Ball et al. 2002) are useful for posing questions and generating hypotheses, but are seldom definitive. Similarly, an argument could be made that our data were from a single landscape (i.e., a small portion of western Minnesota). We are confident that landscape composition, as we defined it, was not related to Mallard clutch size in our nest structures. However, landscape studies are inherently difficult. Levin (1992) reviewed the importance of understanding pattern and scale in ecological studies. We believe that all ecological research should be conducted with the question of landscape scale in mind. Over what scale should the landscape used by a nesting Mallard be defined? Do our results differ from those of Ball and his coworkers because of the scale at which landscapes important to Mallard hens were defined? The idea that landscape composition (or quality) could influence clutch size in waterfowl is intuitively reasonable, and Ball and his coworkers have suggested several possible mechanisms for the influence. We agree that other researchers should examine these relationships for Mallards in other landscapes and for other species in general.

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LITERATURE CITED

Alisauskas, R. T. and C. D. Ankney. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. Pp. 30–61 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). Univ. of Minnesota Press, Minneapolis.

Artmann, M. J., I. J. Ball, and T. W. Arnold. 2001. Influence of perennial upland cover on occupancy of nesting structures by Mallards in northeastern North Dakota. Wildl. Soc. Bull. 29:232–238.

Ball, I. J., M. J. Artmann, and S. T. Hoekman. 2002. Does Mallard clutch size vary with landscape composition? Wilson Bull. 114:404–406.

Greenwood, R. J., A. B. Sargeant, D. H. Johnson, L. M. Cowardin, and T. L. Shaffer. 1995. Factors associated with duck nest success in the prairie pothole region of Canada. Wildl. Monogr. 128: 1–57.

Kleinbaum, D. G., L. L. Kupper, and K. E. Muller. 1988. Applied regression analysis and other multivariable methods, 2nd ed. PWS-KENT, Boston, Massachusetts.

Klett, A. T., H. F. Deubbert, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. Resource Publication 158. U.S. Fish and Wildlife Service, Washington, D.C.

Klomp, H. 1970. The determination of clutch-size in birds: a review. Ardea 58:1–124.

Krapu, G. L., R. J. Greenwood, C. P. Dwyer, K. M. Kraft, and L. M. Cowardin. 1997. Wetland use, settling patterns, and recruitment in Mallards. J. Wildl. Manage. 61:736–746.

Krapu, G. L., A. T. Klett, and D. G. Jorde. 1983. The effect of variable spring water conditions on Mallard reproduction. Auk 100:689–698.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Pinheiro, J. C. and D. M. Bates. 2000. Mixed-effects models in S and Splus. Springer, New York.

Prince, H. 1997. Wetlands of the American Midwest: a historical geography of changing attitudes. Univ. of Chicago Press, Chicago, Illinois.

Reynolds, R. E., D. R. Cohan, and M. A. Johnson. 1996. Using landscape information approaches to increase duck recruitment in the prairie pothole region. Trans. N. Am. Wildl. Nat. Resour. Conf. 61:86–93.

Reynolds, R. E., T. L. Shaffer, R. W. Renner, W. E. Newton, and B. D. J. Batt. 2001. Impact of the Conservation Reserve Program on duck recruitment in the U.S. prairie pothole region. J. Wildl. Manage. 65:765–780.

Rohwer, F. C. 1992. The evolution of reproductive patterns in waterfowl. Pp. 486–539 *in* Ecology and management of breeding waterfowl (B. D. J. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu, Eds.). Univ. of Minnesota Press, Minneapolis.

SAS Institute, Inc. 1989. SAS/IML software: usage and reference, ver. 6. SAS Institute, Inc., Cary, North Carolina.

SAS Institute, Inc. 2000. SAS/STAT users guide, vol. 2, ver. 8.0. SAS Institute, Inc., Cary, North Carolina.

Schaalje, G. B., J. B. McBride, and G. W. Fellingham. 2002. Adequacy of approximations to distributions of test statistics in complex mixed linear models using SAS PROC MIXED. J. Agric. Biol. Environ. Stat. 7:512–524.

Zicus, M. C., D. P. Rave, and M. R. Riggs. 2003. Mass loss from Mallard eggs incubated in nest structures. Wildl. Soc. Bull. 31:270–278.