

GRASSLAND BIRDS ORIENT NESTS RELATIVE TO NEARBY VEGETATION

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ABSTRACT.—We studied orientation of nest sites relative to nearby vegetation for dabbling ducks (Cinnamon Teal, *Anas cyanoptera*; Blue-winged Teal, *A. discors*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; and Northern Shoveler, *A. clypeata*) and Short-eared Owls (*Asio flammeus*) in ungrazed grassland habitat during 1995–1997 in westcentral Montana. We estimated an index of vegetation height and density in intercardinal directions (NE, SE, SW, NW) immediately around nests. All species oriented nests with the least vegetation to the southeast and the most vegetation to either the southwest or northwest. Furthermore, maximum vegetation around nests shifted from the southwest to the northwest with increasing nest initiation date, apparently as a response of individuals tracking seasonal change in the afternoon solar path. Thus, nests were relatively exposed to solar insolation during cool morning hours but were shaded from intense insolation in the afternoon throughout the breeding season. We suggest that nest microhabitat was selected in part to moderate the thermal environment. Received 15 May 2002, accepted 24 August 2002.

Natural selection should favor nest sites that maximize reproduction and survival of adults, and selection of nest microhabitat appears to have evolved in response to predation and microclimate (Walsberg 1981, Gloutney and Clark 1997). Nest microclimate can influence the energetic costs of incubation and the development and survival of eggs and young (Haftorn and Reinertsen 1985, Webb 1987). Many birds select nest microhabitats that ameliorate climatic factors and reduce physiological stress on adults, eggs, and young. Nest sites often are oriented nonrandomly relative to nearby objects or vegetation, presumably to accrue thermal benefits and protection from severe weather (Walsberg 1981, With and Webb 1993, Norment 1993). Birds that construct nests in cavities or with tunnel entrances frequently orient entrances relative to the solar path and prevailing winds (Facemire et al. 1990, Hooge et al. 1999, Wiebe 2001). Orientation of nests relative to surrounding vegetation also has been observed for relatively small-bodied open cup nesters, but large-bodied birds have received little attention (Walsberg 1981, Petersen and Best 1985, With and

Webb 1993, Nelson and Martin 1999). Grasslands birds are exposed to wide daily and seasonal fluctuations in temperature, wind, and moisture, making nest microhabitat especially important. We studied nest microhabitat selection by dabbling ducks (Cinnamon Teal, *Anas cyanoptera*; Blue-winged Teal, *A. discors*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; and Northern Shoveler, *A. clypeata*) and Short-eared Owls (*Asio flammeus*). Specifically, we asked if orientation of nests relative to nearby vegetation differed from random. Based on patterns observed in our data, we also asked if a relative shift in orientation from southwest to northwest occurred with increasing nest initiation date.

METHODS

Study area.—We conducted research on 227 ha of ungrazed grassland habitat in the Mission Valley (47° 24' N, 114° 24' W), 80 km north of Missoula, Montana, during 1995–1997. Glacial topography characterizes the area, which exhibits low relief and high densities of wetlands (Lokemoen 1962). Vegetation was typical of habitat managed for upland-nesting ducks and Ring-necked Pheasants (*Phasianus colchicus*). Plant communities were structurally diverse, dominated by introduced cool season grasses, primarily intermediate wheatgrass (*Agropyron intermedium*), quackgrass (*A. repens*), smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), and orchard grass (*Dactylis glomerata*).

Field methods.—We commenced nest searching in late April and searched twice more at 21- to 25-day intervals using a cable chain device (Higgins et al. 1969). We monitored nests and estimated nest initiation dates following Klett et al. (1986). Observers could not always distinguish between female Cinna-

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TABLE 1. Candidate models examining support for orientation of nests and random locations relative to nearby vegetation and examining support for a seasonal shift in orientation for six species of ground-nesting grassland birds in westcentral Montana, 1995–1997.

Model set	Model ^a	Interpretation
Orientation	Constant	No support for orientation.
	Direction	Orientation by intercardinal direction, consistent across years.
	Direction \times Year	Orientation by intercardinal direction, variable among years.
Shift	Constant	No support for shift.
	Initiation Date	Shift explained by individual response to nest initiation date.
	Median Initiation Date	Shift explained by interspecific differences in nesting phenologies.
	Initiation Date + Species	Shift explained by individual response to nest initiation date, but species differ in orientation for a given date.
	Initiation Date \times Species	Shift varied among species.

^a Models designated by sources of variation in data.

mon and Blue-winged teals, and we assumed that our sample of nests reflected the local predominance of breeding Cinnamon Teal (U.S. Fish and Wildlife Service, National Bison Range unpubl. data). These teal are closely related, physically similar (Johnson and Sorenson 1999), and likely selected similar nest sites. Therefore, we pooled these species (hereafter “teal”) in analyses. We sampled vegetation when nests were no longer active, because we suspected that intensive sampling could increase nest abandonment and provide visual and olfactory cues that may increase nest predation. We assumed that rates of change in vegetation around each nest were similar and that relative differences at the time of sampling reflected patterns at the time of nest site selection. We used a 3.5×3.5 -cm pole alternately marked black and white in 2-cm intervals (modified from Robel et al. 1970) to estimate an index of vegetation height and density (hereafter “vegetation”). From a height of 1 m and a distance of 4 m during 1995 and 2 m during 1996–1997, we recorded (in cm) the lowest visible interval. We shortened the observation distance because we thought that estimates taken from 2 m were more likely to be influenced only by vegetation near the pole. We made estimates while facing nests in the four intercardinal directions (NE, SE, SW, and NW) with the pole centered in the bowl; estimates were calibrated to ground level. We conducted identical sampling at random locations. We identified random locations from a grid superimposed on an aerial photo and then chose each sampling point by tossing a stick in a randomly selected direction. Nest orientation typically has been defined relative to a salient object (e.g., tunnel entrance or stem of nesting shrub) that describes aspect of exposure. Lacking a clearly defined reference object, we defined orientation as nest placement relative to vegetation immediately around nests.

Statistical analyses.—We modeled orientation at nests and random points using General Linear Models

(SPSS, Inc. 2000). We used Akaike’s Information Criterion corrected for sample size (AIC_c) to select parsimonious models for parameter estimation and inference (Burnham and Anderson 1998, Anderson et al. 2000). For each analysis, we created an *a priori* set of candidate models that mathematically represented different biological hypotheses concerning orientation; Akaike weights allowed us to assess relative support among these models. To assess the importance of individual variables, we summed Akaike weights for all models containing a variable.

To examine orientation, we modeled variation in the deviation of estimates of vegetation at each sampling point from the mean for that location. We considered the categorical predictive variables intercardinal direction (Direction) and year (Year). For each species and for random points, we created three *a priori* models to examine support for orientation (Table 1). To examine a perceived seasonal shift in relative vegetation from southwest to northwest, we modeled variation in the difference between estimates in these directions. We hypothesized that orientation shifted in response to seasonal northward change in the solar path and that a shift could result either from response of individuals or interspecific differences. A shift could occur if individuals, regardless of species, altered nest orientation in response to nest initiation date. Thus, we would predict that the individual covariate nest initiation date (Initiation Date) would best explain seasonal change in orientation. Alternatively, if individuals within a species did not alter nest orientation in response to initiation date, a shift could occur if each species selected orientation appropriate to its nesting phenology. Thus, we would predict that the group covariate of median nest initiation date for each species (Median Initiation Date) would best explain seasonal change in orientation. We developed five models to assess support for a shift and, if present, to attempt to distinguish if it was better explained by differences in orientation

TABLE 2. Selection results for models examining orientation of nests relative to nearby vegetation for six species of ground-nesting grassland birds and random locations during 1995–1997 in westcentral Montana. We present results for models with AIC_c weights >0.025.

Group	<i>n</i>	Model ^a	<i>K</i> ^b	log (L) ^c	ΔAIC _c ^d	AIC _c weight ^e
Teal ^f	168	Direction	5	−272.5	0.00	0.93
		Constant	2	−278.2	5.23	0.07
Gadwall	152	Direction	5	−262.9	0.00	0.67
		Constant	2	−266.8	1.42	0.33
Mallard	276	Direction	5	−513.2	0.00	0.54
		Constant	2	−516.5	0.34	0.46
Northern Shoveler	196	Direction	5	−245.1	0.00	0.99
Short-eared Owl	100	Direction	5	−167.3	0.00	0.98
Random	1244	Constant	2	−1,676.7	0.00	0.63
		Direction	5	−1,674.2	1.05	0.37

^a Models designated by source(s) of variation in vegetation immediately around nests.
^b Number of estimated parameters.
^c Maximized log-likelihood.
^d Difference in AIC_c relative to model with lowest value for each group.
^e Weight of evidence for being the best approximating model for each group.
^f Cinnamon and Blue-winged teals pooled.

among species or responses of individuals regardless of species (Table 1). We also considered the categorical predictor species (Species) to estimate potential differences in orientation among species after controlling for a seasonal shift. To assess support for a seasonal shift in orientation at random locations, we considered a constant model versus a model with the continuous covariate date (Date).

RESULTS

Nest orientation.—We included 225 nests in our analyses: 42 teal, 40 Gadwall, 69 Mallard, 49 Northern Shoveler, and 25 Short-eared Owl. Sixty-eight nests were from 1995, 86 from 1996, and 71 from 1997. The Direction model was selected as the best approximating model of orientation for each species (Table 2). Strong support for the Direction model existed for three species (AIC_c weights were >13× those for the next best model). Only moderate support existed for Mallards and Gadwalls (AIC_c weights 1.2–2.0 those for the next best model), but patterns in estimates and effects were similar for all ducks. Vegetation to the southeast of nests was relatively low for all species. Species nesting relatively early (Mallard, Northern Shoveler, and Short-eared Owl) had relatively high vegetation to the southwest of nests, but species nesting relatively late (Gadwall and teal) had relatively high vegetation to the northwest (Fig. 1). For each species, the 95% CI for the difference between directions with highest and lowest estimates did not include zero. For random

points, the Constant model received moderately more support (AIC_c weight 1.7×) than the Direction model (Table 2). Although the Direction model received some support, estimated differences in vegetation among directions from this model were small, and 95% CI's for all estimates overlapped zero (Fig. 1). Direction × Year models received virtually no support (AIC_c weights <0.025).

Seasonal shift in orientation.—Among models examining a seasonal shift in orientation, two models including Initiation Date received similar support as the best approximating model (Table 3). These models received >3× more support than a model including Median Initiation Date, and other models received little support. Summed Akaike weights for models including individual variables provided >6× more support for the predictive importance of Initiation Date (0.85) relative to Median Initiation Date (0.13), indicating that a seasonal shift in orientation was best explained by individual response to nest initiation date. The top model predicted that vegetation to the southwest relative to the northwest of nests decreased ($\beta_1 = -0.128$; 95% CI −0.047, −0.209; *n* = 225) as estimated nest initiation date increased (Fig. 2). The predicted shift in mean vegetation was 10.6 cm across the range of nest initiation dates, and the combined mean for both directions was 24.6 cm. Thus, nearly half (43%) of

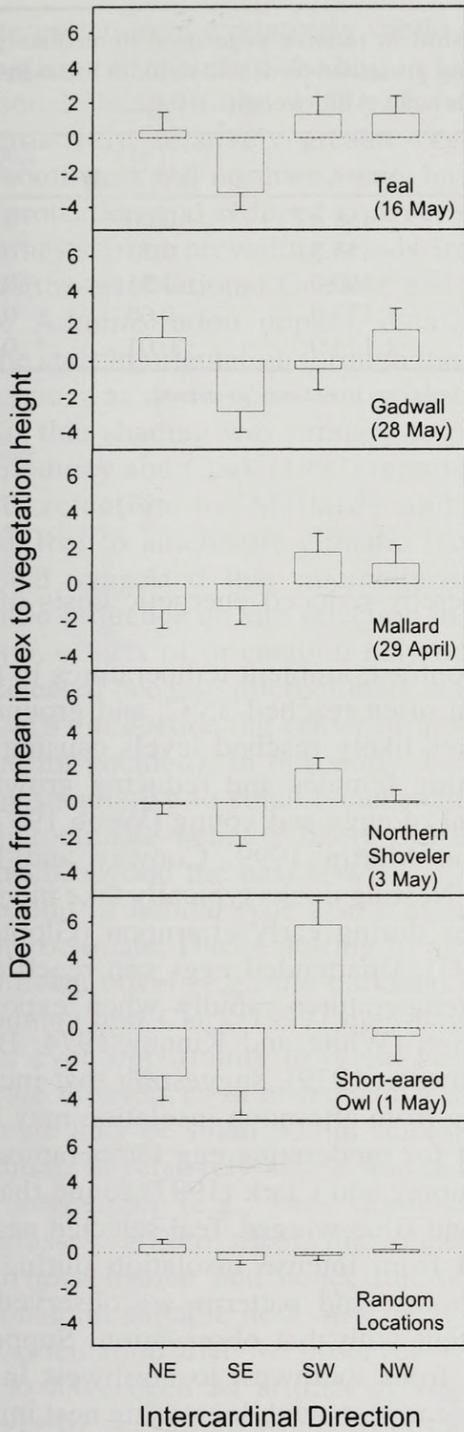


FIG. 1. Deviations (+1 SE) in an index of vegetation height and density in intercardinal directions relative to the mean for that location for nests of six species of ground-nesting grassland birds (median initiation date) and random locations during 1995–1997 in westcentral Montana. Reference lines indicate no difference from mean.

the total vegetation was predicted to shift direction, suggesting that the magnitude of the estimated effect was biologically important. The second best model predicted a more moderate effect of estimated initiation date ($\beta_1 = -0.083$; 95% CI 0.016, -0.181), and differ-

ences in vegetation between southwest versus northwest were predicted to be greater by about 5 cm for Short-eared Owls relative to ducks. In contrast to patterns at nests, support for a seasonal shift at random locations was equivocal (Table 3). The relatively small slope from the Date model ($\beta_1 = -0.031$; 95% CI 0.009, -0.070 ; $n = 616$) could not account for patterns at nests.

DISCUSSION

Microclimate is thought to be an important determinant of nest microhabitat selection for small birds (Walsberg 1985), because they are relatively susceptible to thermal stress. Many small birds appear to orient nest sites to gain thermal benefits (Walsberg 1981, With and Webb 1993, Nelson and Martin 1999). Explanations of nest orientation have focused primarily on optimization of thermal microclimate relative to solar insolation and convective cooling, the major sources of heat exchange at nests (Webb and King 1983). Birds nesting in cool or hot environments may increase or decrease exposure to the sun (Inouye et al. 1981, Finch 1983, Petersen and Best 1985), and birds exposed to wide daily variation in temperature may moderate thermal variation by increasing heat gain in the morning but decreasing it in the afternoon (Walsberg 1981, With and Webb 1993, Hooge et al. 1999, Nelson and Martin 1999). Alternatively, birds may orient nests relative to the prevailing wind to facilitate convective cooling or to reduce exposure to weather (Facemire et al. 1990, Viñuela and Sunyer 1992, Norment 1993).

We believe that support for nest orientation in this study was novel for large-bodied grassland birds, and we suggest that nest sites were selected in part to ameliorate nest microclimate. Consistent patterns of orientation across species suggested common thermal benefits to nest microclimate. The pattern of least vegetation to the southeast and most to the southwest or northwest of nests suggested that birds selected sites that were relatively exposed in the morning to maximize heat gain but shaded in the afternoon to avoid excessive insolation. Energetic costs of incubation increase as ambient temperature declines below a lower critical temperature (T_{lc} ; Haftorn and Reinertsen 1985). Assuming body temperatures of 40°C

TABLE 3. Selection results for models examining seasonal shift in relative vegetation immediately to the southwest versus northwest of nests of six species of ground-nesting grassland birds and random locations during 1995–1997 in westcentral Montana. We present results for models with AIC_c weights >0.02.

Group	Model ^a	K ^b	log (L) ^c	ΔAIC _c ^d	AIC _c weight ^e
Nest	Initiation Date	3	−458.8	0.00	0.45
	Initiation Date + Species	6	−455.7	0.23	0.40
	Median Initiation Date	3	−460.0	2.51	0.13
Random	Date	3	−1,173.0	0.00	0.50
	Constant	2	−1,174.0	<0.01	0.50

^a Models designated by source(s) of variation in difference (southwest – northwest) of vegetation immediately around nests.
^b Number of estimated parameters.
^c Maximized log-likelihood.
^d Difference in AIC_c relative to model with the lowest value for each group.
^e Weight of evidence for being the best approximating model for each group.

and typical masses for breeding females, estimated T_{lc} for our study species ranged between about 10° C for Mallards to about 16° C for teal (Calder and King 1974: equation 20). Ambient temperatures on our study area early in the nesting season or at night typically were below T_{lc} of females. Similarly, temperatures at nests of Mallards and Blue-winged Teal have been demonstrated to be below their T_{lc} for most of the night (Gloutney and Clark 1997). Selecting nests with relatively high southeast exposure likely facilitated heat gain during the morning (Nelson and Martin 1999)

and thereby reduced energetic costs of incubation.

In contrast, ambient temperatures in the afternoon often reached 35°C, and ground temperatures likely reached levels causing stress to nesting females and reducing growth and survival of eggs and young (Webb 1987, Nelson and Martin 1999, Conway and Martin 2000). Nesting ducks typically take incubation recesses during early afternoon (Gloutney et al. 1993). Unattended eggs can reach deleterious temperatures rapidly when exposed to insolation (White and Kinney 1974, Bennett and Dawson 1979), suggesting that increased shading from afternoon insolation may be important for moderating egg temperature.

Gloutney and Clark (1997) found that Mallards and Blue-winged Teal selected nest sites shaded from intense insolation during afternoon hours, and patterns we observed were consistent with that observation. Support for a shift from southwest to northwest in vegetation near nests with increasing nest initiation dates suggested that individual females tracked seasonal changes in the solar path when selecting nest sites. When nesting began in early April, the sun was in the southern hemisphere of the sky for most of the day. However, the sun was near its northernmost extent from late May to the end of July, spending nearly half of the afternoon in the northern hemisphere of the sky and setting to the northwest. Others have observed relatively abrupt seasonal switches from nest orientations increasing to those decreasing heat gain as ambient temperatures increased (Austin 1976, Finch 1983). However, we believe that

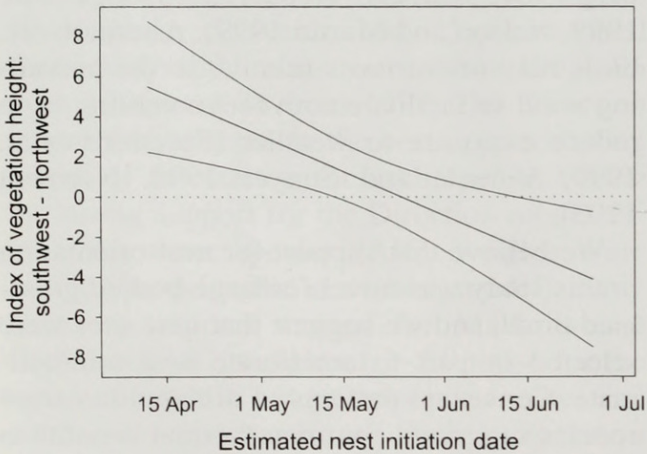


FIG. 2. Difference between an index of vegetation height and density immediately to the southwest and the northwest of nests of dabbling ducks (Cinnamon Teal, *Anas cyanoptera*; Blue-winged Teal, *A. discors*; Gadwall, *A. strepera*; Mallard, *A. platyrhynchos*; and Northern Shoveler, *A. clypeata*) and Short-eared Owls (*Asio flammeus*) relative to estimated nest initiation date during 1995–1997 in westcentral Montana, with 95% CI for predicted mean values. Positive values indicate more vegetation to the southwest relative to the northwest; dotted line indicates no change over time.

our interpretation of a relatively subtle change in orientation to maintain shading in response to seasonal change in the solar path is novel.

Alternatively, relatively greater vegetation to the southwest and northwest may have provided protection and reduced convective heat loss at nests from prevailing winds from the west-northwest (National Oceanic and Atmospheric Administration unpubl. data). However, the shift in orientation through the breeding season was more consistent with the hypothesis that shading was primary to orientation. Gloutney and Clark (1997) reported only limited selection by Mallards and Blue-winged Teal to ameliorate climatic factors at nests and suggested that microclimate may have little influence on site selection in ducks. However, effects of orientation may not have been detected because microclimate was measured >10 cm outside the center of nests (orientation unspecified). In our study, birds oriented nests relative to small bunches of grass, and microclimate benefits likely did not extend much beyond the nest bowl.

Selection of habitat type also may ameliorate microclimate. Ducks nesting in relatively tall, uniform cover (e.g., the parkland habitat in Gloutney and Clark 1997) may have little need or even opportunity to orient nests, and fine scale differences in microhabitat and microclimate may be small within suitable nesting habitat. In relatively sparse and heterogeneous vegetation (e.g., sites dominated by bunchgrasses, grazed sites), fine scale variation in microhabitat and hence microclimate may constrain suitable nest sites.

The orientation that we observed was unlikely to have been an artifact of vegetation bent over by prevailing winds from the west-northwest, as no comparable differences occurred at random locations. Alternatively, nests under blown down vegetation may have been selected for overhead cover rather than orientation *per se*. However, Mallards and teal nested almost exclusively in bunchgrasses with stiff stems and leaves that were not prone to blowing over; in addition, Short-eared Owls selected for almost no overhead cover (STH unpubl. data) but showed the strongest orientation of vegetation around nests.

Ultimately, birds should select nest sites that minimize reproductive failure and hence maximize fitness. Nests that deviate from the

typical orientation at a site often experience decreased reproductive success (Austin 1976, Högstedt 1978, Viñuela and Sunyer 1992, Hooge et al. 1999, Wiebe 2001). Predation is the primary cause of nest failure in most birds (Martin 1993). Most studies of nest microhabitat selection by grassland birds have focused on the relationship between concealment and predation, thereby tacitly assuming that microhabitat selection responds primarily to predation pressure (Clark and Nudds 1991, DeLong et al. 1995). Unsuitable nest microclimates could increase energetic needs of adults and hence decrease nest attentiveness, which could prolong exposure to predation (White and Kinney 1974, Webb 1987, Yanes et al. 1996, Loos 1999) or increase vulnerability of nests to predators (Högstedt 1978, Martin et al. 2000a, 2000b). Further study of selection of nest microhabitat in grasslands will be needed to determine consequences for nest microclimate, parental energetics and behavior, and reproductive success.

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