

NEST-SITE SELECTION BY MALLARDS AND BLUE-WINGED TEAL IN RELATION TO MICROCLIMATE

MARK L. GLOUTNEY^{1,3} AND ROBERT G. CLARK^{1,2}

¹ Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, Saskatchewan S7N 5E2, Canada; and

² Canadian Wildlife Service, Prairie and Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, Saskatchewan S7N 0X4, Canada

ABSTRACT.—It is unclear whether female ducks select nest sites on the basis of microclimatic features. Therefore, we tested the nest microclimate selection hypothesis by concurrently monitoring temperature (T), solar insolation, and relative humidity (RH) at Mallard (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*) nest sites and nearby randomly selected “nonnest” sites (hereafter “adjacent” sites). Operative temperatures (T_e) were calculated for nest sites and adjacent sites. Mallard and teal nest sites received consistently less insolation than adjacent sites, but did not differ in T or RH. T_e at Mallard nest sites was more moderate than at adjacent sites; nest sites were cooler between 0800 and 1730 CST. This pattern did not exist for teal nest sites, which had consistently lower T_e throughout daylight hours. Coefficients of variation for all microclimatic variables did not differ between Mallard and teal nest sites and adjacent sites. We examined interspecific differences in nest-site microclimate by matching data by date and stage of incubation. Teal nest sites received more insolation and experienced greater T_e than concurrently monitored Mallard nest sites, but there were no interspecific differences in T or RH. Our results provide only limited support for the microclimatic selection hypothesis, suggesting that other factors are more important determinants of nest-site selection in ducks. Received 20 June 1996, accepted 24 January 1997.

SELECTION OF A NEST SITE is a critical component of avian reproduction because it determines the environment to which the parent and eggs will be exposed for a relatively long period, and it presumably has evolved in relation to predation, local availability of resources, and microclimate. In this paper, we focus on the influence of microclimate because maintenance metabolism accounts for 40 to 60% of total daily energy expended (Walsberg 1983a), and thermal regimes of an animal's microhabitat potentially can have a strong influence on energetic costs (Gabrielsen and Unander 1987, Novoa et al. 1990, Warkentin and West 1990, Gabrielsen et al. 1991, Swain 1991). Therefore, energy saved from appropriate nest-site choices can be channeled to other activities such as reproduction.

Ducks typically experience low nesting success (Greenwood et al. 1995, Sovada et al. 1995, Beauchamp et al. 1996) and generally select nest sites that provide some degree of conceal-

ment (Klett et al. 1988, Greenwood et al. 1995). However, Clark and Nudds (1991) demonstrated that the fate of duck nests could not be determined solely on the basis of nest concealment. Although it is clearly beneficial to nest in areas with some cover, benefits in terms of increased nesting success within areas of “suitable” cover are not apparent. Therefore, ducks may use other cues in combination with concealment when selecting nest sites.

One of the most common examples of microhabitat selection in birds is nonrandom distribution of nests in dense vegetation. Although nests located in dense vegetation are thought to be less vulnerable to predation (Patterson 1980, Cody 1985, Rands 1988, Filliater et al. 1994), they also benefit from protection from wind, nocturnal radiative heat loss, and diurnal heat gain (Walsberg 1981, 1985; Colwell 1992). Nesting birds can respond to climatic extremes by: (1) selecting appropriate microclimates in which to nest, (2) adapting nest structure to prevailing climatic factors, and (3) using behaviors such as shading to protect eggs (Horvath 1964). Site selection for thermal advantages has been proposed to explain nonrandom nest-site placement in a variety of species (e.g.

³ Present address: Stanley Consulting Group Ltd., 108–3502 Taylor Street East, Saskatoon, Saskatchewan S7H 5H9, Canada.
E-mail: stanley.sktn@stantech.com

Kern and van Riper 1984, Bekoff et al. 1987, van Riper et al. 1993).

During incubation, birds often subject themselves to severe heat loading, either from direct solar radiation or from convective and conductive heat exchanges (e.g. Bartholomew and Dawson 1979, DeJong 1979, Goldstein 1984). Therefore, selection of favorable nest microclimates can have important consequences for the energetics of nesting birds (Calder 1973, Austin 1974). Many studies have demonstrated that the vegetational and structural characteristics of microhabitats surrounding nests differ from those at randomly selected sites (e.g. Holway 1991, Sakai and Noon 1991, Tuomenpuro 1991, Sedgwick and Knopf 1992); however, few studies have measured microclimatic variables at nests and adjacent sites. Accordingly, we measured temperature, solar insolation, and relative humidity at nests of Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*; hereafter "teal") and compared these data with the same measurements taken at nearby randomly selected "nonnest" sites (hereafter "adjacent" sites).

Studies have shown that the energetic costs of incubation typically increase linearly as ambient temperature declines below the lower critical temperature (T_{lc} ; the temperature below which animals must generate extra heat to maintain body temperature; see Ricklefs 1974, Turner 1993). Therefore, thermal considerations should result in animals selecting microhabitats that reduce exposure to conditions below T_{lc} . Body size impinges on virtually all aspects of an animal's physiological ecology. Body mass averages 900 g for Mallards and 350 g for Blue-winged Teal, which translates to a T_{lc} of 9.5°C and 16.5°C, respectively (Calder and King 1974: equation 20; assuming a body temperature of 40°C). The small size of teal may result in their having proportionately higher energetic costs of incubation than Mallards because their (1) mass-specific metabolic rate is higher (Calder 1974); (2) clutch mass represents a 28% greater proportion of their body mass (Gloutney 1989); (3) reliance on food resources to meet costs of incubation is greater (Afton and Paulus 1992); and (4) daily recess frequency is three times greater than that of Mallards (Gloutney 1996). Therefore, teal may be more responsive than Mallards to mechanisms that reduce the costs of incubation.

The objective of our study was to evaluate microclimatic consequences of nest-site selection to incubating female ducks. Specifically, we tested the microclimatic selection hypothesis (MSH), which states that nest sites are selected to minimize the physiological "stress" of incubation to females (see With and Webb 1993). Under the assumption that nest-site selection is based primarily on microclimatic considerations, we predicted that: (1) temperature (normal and operative [see below]) and relative humidity at nest sites will be more moderate and less variable than at adjacent sites; and (2) nest sites will be more shaded than adjacent sites. These predictions are based on the premise that birds should select nest sites that reduce nocturnal heat loss and diurnal heat gain and that excessive humidity decreases the convective cooling ability of females. Furthermore, the MSH predicts that nest sites should experience temperatures below T_{lc} less frequently than adjacent sites (temperatures rarely exceeded 38°C on our study area, so we did not evaluate upper critical temperatures). Furthermore, we evaluated microclimatic consequences of interspecific differences in nest-site selection. If microclimatic conditions are more important determinants of nest-site selection in teal than in Mallards, then compared with Mallards, the small-bodied teal should select nest sites with: (1) a more restricted range of microclimates, and (2) higher operative temperatures than occur at Mallard nest sites.

STUDY AREA AND METHODS

The study was conducted in parkland habitat on and near the St. Denis National Wildlife Area (52°13' N, 106°04' W) in Saskatchewan, Canada, from 1990 to 1992 (see Sugden and Beyersbergen 1985). Mallard and teal nests were located during three systematic searches from early May to mid-July and incidentally during daily field work. Herbaceous cover was searched using standard cable-drag techniques (Klett et al. 1986), whereas shrubs and aspen (*Populus* spp.) groves were searched on foot (Clark et al. 1991). Cropland and flooded wetlands usually were not searched. Searches were conducted between 0800 and 1400 CST (Gloutney et al. 1993).

Habitat classification.—Vegetation was characterized within 30 cm of nests and adjacent sites, and mean canopy height was recorded. Habitat types were determined for each nest site and adjacent site based on gross features. Habitats included: (1) aspen groves, (2) tall shrubs (mean canopy height >50 cm),

(3) short shrubs (mean canopy height ≤ 50 cm), (4) tall grass (mean canopy height > 30 cm), (5) short grass (mean canopy height ≤ 30 cm), and (6) pond edge (i.e. unflooded moist soil zones surrounding wetlands). Although Mallards occasionally build nests over water (Arnold et al. 1993), we did not collect microclimatic data at such nests.

Microclimatic variables.—Temperature ($\pm 0.1^\circ\text{C}$), relative humidity ($\pm 2\%$), and insolation ($\pm 3\%$, $\text{W}\cdot\text{m}^{-2}$) were measured at nest sites and associated adjacent sites using Campbell Scientific (CSI) 21X dataloggers equipped with CSI 207 temperature/relative humidity probes and LI200S Licor pyranometers (spectral range, 0.4 to 1.2 μm ; sensitivity, $80 \mu\text{A}/1,000 \text{W}\cdot\text{m}^{-2}$). One set of probes was placed 5 cm from the edge of an active duck nest while the remaining sets of probes were located at two types of adjacent sites: (1) a *matched site*, randomly located within the same habitat as the duck nest; and (2) a *random site*, randomly located within any habitat. Adjacent sites were chosen by blindly throwing a marker after traveling a random distance (1 to 60 m) along a random bearing from the nest. Probes were arranged along a north/south axis, with pyranometers always located south of the CSI 207 probe to avoid shading. Probes were separated by 8 to 10 cm at matched and random sites. Pyranometers were level and faced the sky. CSI 207 probes were located 6 cm above ground and sensors from pyranometers 2 cm above ground. Wind speed ($\pm 0.5 \text{ m/s}$) was measured within 15 m of nest sites at a height of 3 m with a Young Wind Sentry 3101-5 anemometer. Prior to each season, simultaneous recordings from each sensor under similar conditions were statistically equal ($P > 0.05$). All adjacent sites were located within 60 m of duck nests. Dataloggers recorded 30-min means and standard deviations based on 5-s measurement intervals. Data were recorded at each setup for six to seven days.

Air temperature alone is insufficient to characterize an incubating bird's thermal environment because wind speed, solar insolation, and vapor pressure interact with temperature in a complex fashion (Fanger 1970, McArthur 1990). Consequently, we calculated operative temperature (T_e), which integrates the effects of air temperature, solar insolation, and convective heat flow (Robinson et al. 1976, Campbell 1977). T_e is a more appropriate measure of microclimate than either temperature or solar insolation because differences between body temperature and T_e represent the thermal gradient between the animal and its environment. We calculated T_e for each nest and adjacent site (calculation details provided in Appendix).

Microclimatic data were matched by date and 30-min time block for concurrently monitored pairs of Mallard and teal nest sites. Data were further restricted to situations where both species were at similar stages of incubation (± 3 days). In this way, we

assessed differences between species under identical ambient conditions while controlling for stage of nesting.

Statistical analyses: Nests versus adjacent sites.—Data were summarized as means and coefficients of variation for each microclimatic site (nest, matched, and random) and time block (30-min period). Analyses were performed separately for the periods of daylight (0500 to 2200) and darkness (2230 to 0430). We adopted this approach because there is no insolation at night. Furthermore, we lacked sufficient data from teal to perform the analysis for the entire day.

Due to lack of independence (i.e. multiple measurements at the same site for several days), we used repeated measures multivariate analysis of covariance (MANCOVA) to test for differences in microclimatic variables between nest sites and adjacent sites (Beal and Khamis 1990, Bogartz 1994). In addition to accounting for multiple measurements at the same site, a repeated-measures approach provides a test for interactions between within-subject (i.e. time) and between-subject (i.e. site) effects (see Milliken and Johnson 1984, Bogartz 1994). MANCOVA also simultaneously tests for significance of effects for more than one dependent variable. One drawback of repeated measures MANCOVA is that it can have low power to detect treatment effects. However, use of univariate repeated measures can result in Type I errors (Milliken and Johnson 1984). To guard against low power, visual inspections of data were used to confirm statistical results.

Each model initially contained four explanatory variables (site, habitat, date, year), a site \times nest interaction, and all higher-order interactions. Complete models (Type III SS) were run including all explanatory variables and interactions. We then used a hierarchical procedure in which the highest level, nonsignificant interactions were deleted and the analysis was rerun (Alisauskas and Ankney 1994). The treatment variable (i.e. site) was retained in all models. Reduced models contained only significant explanatory variables and interactions. F -values reported from MANCOVA were determined using Wilks' criterion. All analyses were executed on SAS (SAS Institute Inc. 1990).

The proportion of time temperatures fell below T_{lc} was determined for each nest site and associated adjacent site. Differences in T_{lc} among nest sites, matched sites, and random sites were evaluated with Kruskal-Wallis tests (χ^2 approximation; Siegel and Castellan 1988).

Statistical analyses: Interspecific comparisons.—Data were summarized as means and coefficients of variation for each nest and time block. Due to lack of data independence, we used repeated measures analysis of covariance (ANCOVA, Type III SS) to test for differences between Mallards and teal in nest microclimatic variables (Bogartz 1994). A univariate repeated measures approach was employed because of lim-

TABLE 1. *F*-values (repeated measures MANCOVA) for differences in means and coefficients of variation (CV) in temperature between nest sites and adjacent matched and random sites for Mallards and Blue-winged Teal. Analyses restricted to daylight hours (0500 to 2200); df identical for analyses of mean and CV.

	Mallard			Blue-winged Teal		
	df	\bar{x}	CV	df	\bar{x}	CV
Site	2	0.5	0.7	2	0.2	0.24
Site within nest		ns	ns		ns	ns
Habitat	5	6.8***	8.3***	2	ns	ns
Date	1	29.0***	82.7***	1	5.8**	34.9***
Year	2	43.1***	96.7***	2	ns	18.7***
Hour	34, 49	10.4***	13.0***	34, 3	5.8*	15.8**
Hour × site	68, 98	1.3	1.7**	68, 6	2.3	0.9
Hour × nest × site		ns	ns		ns	ns
Hour × habitat	170, 248	6.0***	7.1***	68, 6	15.8***	ns
Hour × date	34, 49	7.6***	11.8***	34, 3	ns	13.9**
Hour × year	68, 98	8.7***	16.7***	68, 6	ns	4.6**

*, *P* < 0.1; **, *P* < 0.05; ***, *P* < 0.01; ns, *P* > 0.1 (excluded from model).

ited degrees of freedom. Univariate repeated measures ANCOVA require that data exhibit a Type H covariance pattern. Sphericity tests revealed that data did not exhibit this type of matrix (SAS, Proc GLM). Consequently, numerator and denominator degrees of freedom were adjusted using Greenhouse-Geisser ϵ (SAS, Proc GLM). Analyses involving insolation were restricted to periods of daylight. Complete models were run with all explanatory variables and interactions. We followed hierarchical procedures outlined above, with the treatment variable (i.e. species) being retained in all models.

RESULTS

Data were collected at 32 Mallard and 14 teal nest sites, and at 92 adjacent sites. Mallard and

teal nest sites (and their adjacent sites) were monitored for 251 and 107 days, respectively.

Nests versus adjacent sites during daytime.—The results we report follow statistical control of significant annual, seasonal, and temporal variation in microclimatic variables (Tables 1 to 4). We found no significant differences in mean temperature, relative humidity, and their coefficients of variation between Mallard nest sites and adjacent sites during daylight hours (Tables 1 and 2, Fig. 1). Mallard nest sites and adjacent sites differed significantly in mean exposure to solar insolation, but coefficients of variation did not differ between nest sites and adjacent sites (Table 3, Fig. 1). Mallard nest sites received consistently less solar insolation

TABLE 2. *F*-values (repeated measures MANCOVA) for differences in means and coefficients of variation (CV) in relative humidity between nest sites and adjacent matched and random sites for Mallards and Blue-winged Teal. Analyses restricted to daylight hours (0500 to 2200); df identical for analyses of mean and CV.

	Mallard			Blue-winged Teal		
	df	\bar{x}	CV	df	\bar{x}	CV
Site	2	0.5	0.5	2	0.07	0.03
Site within nest		ns	ns		ns	ns
Habitat	5	4.1***	10.9***	2	5.4***	8.5***
Date	1	9.1***	27.2***	1	7.9***	14.0***
Year	2	8.1***	7.1***	2	17.3***	43.1***
Hour	34, 49	14.5***	16.4***	34, 3	153.5*	14.8
Hour × site	68, 98	1.1	0.9	68, 6	3.4	0.4
Hour × nest × site		ns	ns		ns	ns
Hour × habitat	170, 248	7.4***	6.9***	68, 6	50.2**	15.3*
Hour × date	34, 49	10.5***	12.4***	34, 3	91.8*	ns
Hour × year	68, 98	14.6***	12.0***	68, 6	18.2*	21.0**

*, *P* < 0.1; **, *P* < 0.05; ***, *P* < 0.01; ns, *P* > 0.1 (excluded from model).

TABLE 3. *F*-values (repeated measures MANCOVA) for differences in means and coefficients of variation (CV) in insolation between nest sites and adjacent matched and random sites for Mallards and Blue-winged Teal. All analyses restricted to daylight hours (0500 to 2200); df identical for analyses of mean and CV.

	Mallard			Blue-winged Teal		
	df	\bar{x}	CV	df	\bar{x}	CV
Site	2	8.8***	2.2	2	0.99	0.8
Site within nest		ns	ns		ns	ns
Habitat	5	6.0***	ns	2	ns	3.9**
Date	1	ns	9.8***	1	ns	ns
Year	2	ns	8.7***	2	4.3**	6.4***
Hour	34, 49	10.0***	6.6***	34, 3	5.4**	2.3
Hour × site	68, 98	2.1***	1.1	68, 6	0.9	0.9
Hour × nest × site		ns	ns		ns	ns
Hour × habitat	170, 248	2.0***	ns	68, 6	ns	5.2*
Hour × date	34, 49	ns	5.6***	34, 3	ns	ns
Hour × year	68, 98	ns	3.2***	68, 6	2.6*	4.1*

*, *P* < 0.1; **, *P* < 0.05; ***, *P* < 0.01; ns, *P* > 0.1 (excluded from model).

between 0530 and 2130 than did random sites (Duncan's multiple range test, *P* < 0.05; Fig. 1) but did not differ from matched sites during these hours (*P* > 0.05; Fig. 1).

T_e at Mallard nest sites differed significantly from *T_e* at adjacent sites during daylight hours (Table 4, Fig. 1), but there were no differences in coefficients of variation in *T_e* between Mallard nest sites and adjacent sites (Table 4, Fig. 1). *T_e* was significantly greater at random sites than at Mallard nest sites between 0800 and 1730 (Duncan's multiple range test, *P* < 0.05; Fig. 1), but was statistically equal at Mallard nests and matched sites during this period (*P* > 0.05; Fig. 1).

In contrast, we found no significant differences in mean temperature, relative humidity,

insolation, and *T_e* between teal nest sites and their adjacent sites during the day (Tables 1 to 4, Fig. 2). Furthermore, there were no significant differences in the coefficients of variation of these variables between teal nest sites and adjacent sites during this period (Tables 1 to 4, Fig. 2).

Insolation averaged 30% lower and *T_e* 5°C cooler at Mallard nest sites than at random sites during the hottest time of day (i.e. 1400). Similarly, insolation was 30% lower and *T_e* was 3.3°C cooler at teal nest sites than at matched sites. Therefore, both species appeared to select nest sites that provided protection from the intense midday sun.

Nests versus adjacent sites during nighttime.—The results we report follow statistical control

TABLE 4. *F*-values (repeated measures MANCOVA) for differences in means and coefficients of variation (CV) in operative temperature between nest sites and adjacent matched and random sites for Mallards and Blue-winged Teal. Analyses restricted to daylight hours (0500 to 2200); df identical for analyses of mean and CV.

	Mallard			Blue-winged Teal		
	df	\bar{x}	CV	df	\bar{x}	CV
Site	2	5.7***	0.6	2	0.7	0.18
Site within nest		ns	ns		ns	ns
Habitat	5	7.7***	3.9***	2	ns	6.1***
Date	1	7.4***	60.9***	1	ns	10.2***
Year	2	14.9***	55.2***	2	ns	11.5***
Hour	34, 49	21.2***	12.6***	34, 3	2,434.6***	3.8
Hour × site	68, 98	1.5**	1.6**	68, 6	0.7	1.5
Hour × nest × site		ns	ns		ns	ns
Hour × habitat	170, 248	3.2***	3.7***	68, 6	ns	ns
Hour × date	34, 49	4.0***	8.6***	34, 3	ns	ns
Hour × year	68, 98	5.0***	7.5***	68, 6	ns	ns

*, *P* < 0.1; **, *P* < 0.05; ***, *P* < 0.01; ns, *P* > 0.1 (excluded from model).

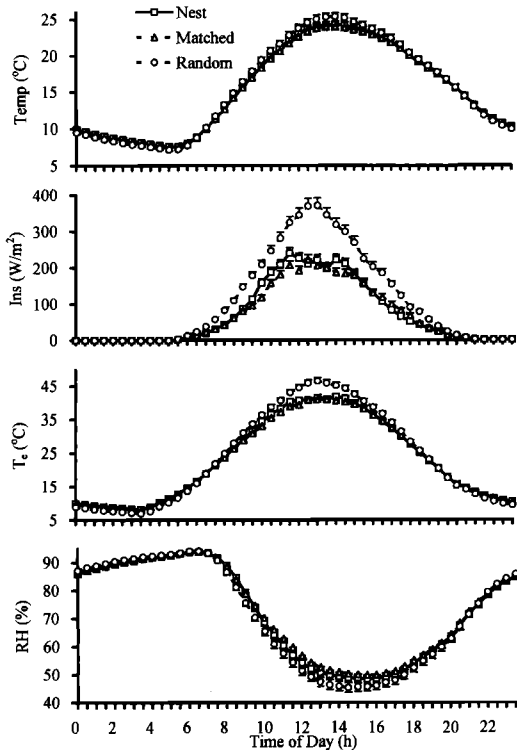


FIG. 1. Temperature (Temp), insolation (Ins), operative temperature (T_e) and relative humidity (RH) at Mallard nest sites, matched sites, and random sites ($\bar{x} \pm SE$).

of significant annual, seasonal, and temporal variation in microclimatic variables. We found no significant differences in mean temperature, relative humidity, and T_e between both Mallard and teal nest sites and their adjacent sites during hours of darkness (Mallard: maximum $F = 0.54$, minimum $P = 0.58$; teal: maximum $F = 0.5$, minimum $P = 0.59$; Figs. 1 and 2). Furthermore, there were no significant differences in coefficients of variation of these variables between both Mallard and teal nest sites and their adjacent sites (Mallard: maximum $F = 1.6$, minimum $P = 0.2$; teal: maximum $F = 0.09$, minimum $P = 0.92$; Figs. 1 and 2).

Lower critical temperature.—If ducks select sites for microclimatic advantages (i.e. avoidance of conditions below T_{lc}), then nest sites would experience these conditions less frequently than would matched sites or random sites. There were no significant differences in the amount of time that temperatures at nest sites, matched sites, and random sites were be-

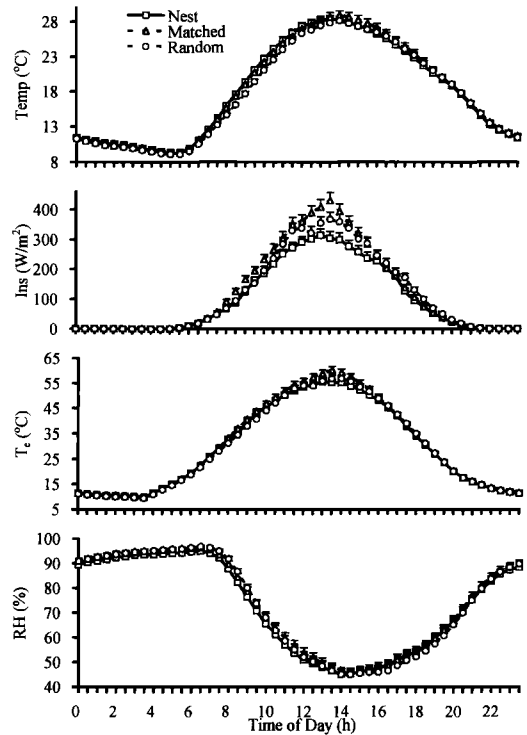


FIG. 2. Temperature (Temp), insolation (Ins), operative temperature (T_e) and relative humidity (RH) at Blue-winged Teal nest sites, matched sites, and random sites ($\bar{x} \pm SE$).

low predicted T_{lc} for Mallards (nest: 25.2%, matched: 25.5%, random: 25.4%) or for teal (nest: 50.3%, matched: 49.6%, random: 52.2%; Kruskal-Wallis tests, Mallard: $\chi^2 = 0.06$, $df = 2$, $P = 0.97$; teal: $\chi^2 = 1.04$, $df = 2$, $P = 0.59$).

Interspecific comparisons.—We recorded microclimatic variables concurrently for 63 nest days at 15 pairs of Mallard and teal nest sites ($\bar{x} = 4.1 \pm SD$ of 2.1 days/pair, range 2 to 8 days/pair) in all habitats (Mallards: 5 nests in short shrubs, 6 in tall grass, 2 in short grass, 2 in pond edge; teal: 9 nests in tall grass, 4 in short grass, 2 in pond edge). The results we report follow statistical control of significant annual, seasonal, and temporal variation in microclimatic variables (Table 5). Mean temperature, relative humidity, and their coefficients of variation did not differ between Mallard and teal nest sites (Table 5, Fig. 3). Teal nest sites received more insolation and had significantly greater T_e than did Mallard nest sites (Table 5, Fig. 3); however, the coefficient of variation of

TABLE 5. F-values (repeated measures ANCOVA) of differences in temperature, relative humidity, insolation, operative temperature, and relative humidity between concurrently monitored Mallard and Blue-winged Teal nest sites. Analyses of differences in mean values and in coefficients of variation (CV), including all hours of the day, insolation restricted to daylight hours (0500 to 2200); df identical for analyses of mean and CV.

	Temperature			Relative humidity			Insolation			Operative temperature		
	df	\bar{x}	CV	df	\bar{x}	CV	df	\bar{x}	CV	df	\bar{x}	CV
Species	1	1.4	0.3	1	0.5	0.01	1	6.8**	0.01	1	96.1***	0.98
Pair	14	19.8***	17.1***	14	12.8***	ns	14	13.6**	1.9**	14	8.2***	23.2***
Hour	47	1,171***	114.6***	47	1,131***	21.8***	34	72.5***	72.4***	47	922.2***	134.6***
Hour × species	47	1.7	0.4	47	1.1	0.04	34	2.9*	0.01	47	26.6***	1.4
Hour × pair	658	5.6***	8.6***	658	8.8***	ns	434	2.0**	2.0**	658	3.0***	7.7***

*, P < 0.1; **, P < 0.05; ***, P < 0.01; ns, P > 0.1 (excluded from model).

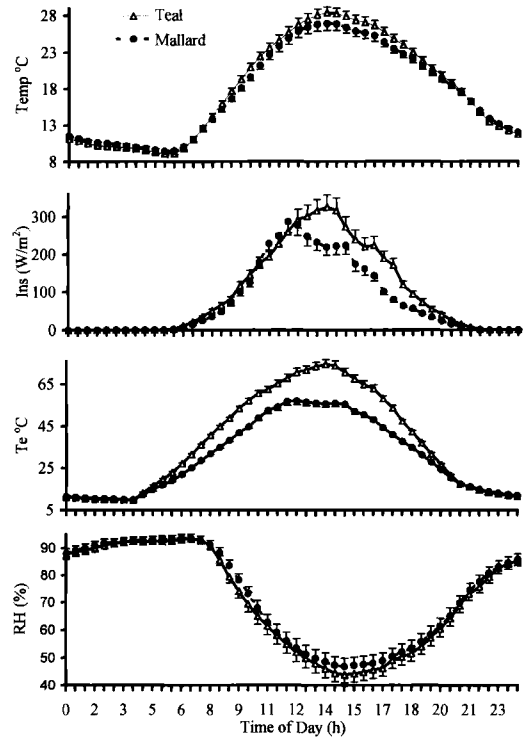


FIG. 3. Temperature (Temp), insolation (Ins), operative temperature (T_e) and relative humidity (RH) at Blue-winged Teal and Mallard nest sites, matched by date and stage of incubation ($\bar{x} \pm SE$).

insolation and T_e did not differ at nest sites of the two species (Table 5).

Analyses were repeated using data from paired nests of both species that were in tall grass (5 pairs, 18 nest days). Results were identical to those reported above, indicating that within the same habitat, teal selected nest sites that received more insolation and consequently exhibited higher T_e than did Mallard nest sites.

Temperature and embryonic development.—Physiological zero temperature is the egg temperature below which no embryonic development occurs (ca. 25°C; Haftorn 1988). Egg temperatures above 41°C are lethal to embryos (Drent 1975). Thirty-min mean nest-site temperatures at both Mallard and teal nest rarely exceeded 38°C (<0.1% of the 12,048 and 5,136 time blocks for Mallards and teal, respectively). However, nest temperatures fell below 25°C for 86% and 78% of the time at Mallard and teal nest sites, respectively. Temporal patterns revealed that temperatures at both Mallard and teal nest

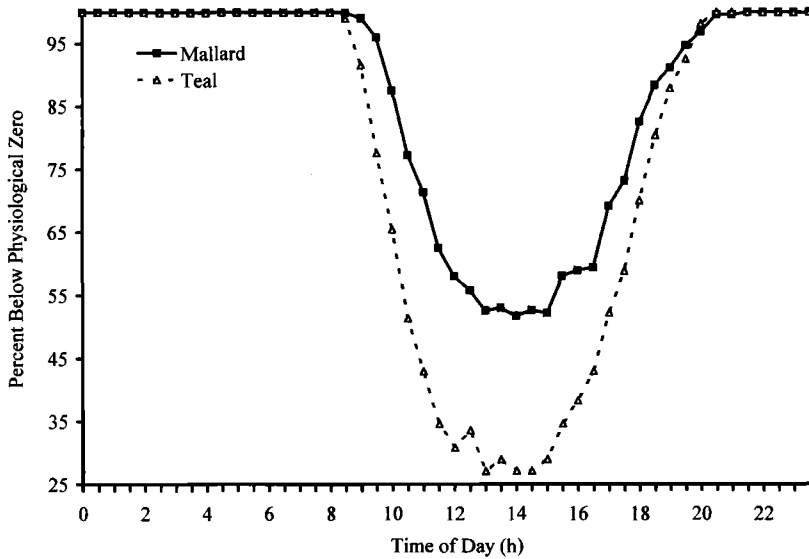


FIG. 4. Percent of 30-min mean temperature blocks at Blue-winged Teal and Mallard nest sites that were below physiological zero temperature (25°C).

sites on average were above physiological zero from 1100 to 1800 (Fig. 4).

DISCUSSION

The data from Mallards provided mixed support for the MSH. Although we found no difference in temperature or relative humidity between nest sites and adjacent sites, nest sites received less insolation and experienced lower T_e than associated random sites. Nest-site selection appears to occur at the habitat-patch level because microclimatic conditions at nest sites and matched sites (i.e. sites within the same habitat patch) did not differ. Results for Blue-winged Teal clearly did not support the MSH, because microclimatic conditions at nest sites and adjacent sites were not statistically different. On average, however, teal nest sites received less insolation through midday than did associated matched sites, suggesting that teal selected nest sites at a finer habitat scale (i.e. within-patch selection) than Mallards. Fine-scale selection may arise because teal nest within a more restricted range of habitats than Mallards (Greenwood et al. 1995, Gloutney 1996). Alternatively, physical processes related to body size, such as metabolic rates, heat loading (surface area to volume), and reliance on endogenous reserves may force teal to be more responsive to thermal environments than are

Mallards. Indeed, under identical ambient conditions, teal nest sites received greater insolation and experienced substantially elevated T_e relative to Mallard nest sites, even when both species nested within the same habitat.

Nest placement may be influenced by solar insolation (Clark et al. 1990, Sakai and Noon 1991, van Riper et al. 1993, With and Webb 1993). Indeed, homeotherms can reduce energy costs of thermoregulation by behaviorally exploiting sources and sinks of radiation of various wavelengths (e.g. Sakai and Noon 1991, Walsberg 1992, van Riper et al. 1993). For example, White-crowned Sparrows (*Zonotrichia leucophrys*) responded to experimentally declining temperatures by selecting locations with greater radiation (DeJong 1976, Mahoney and King 1977). Conversely, many species select nest sites that reduce exposure to midday insolation (e.g. Walsberg 1981; Clark et al. 1983, 1990; Sakai and Noon 1991; this study).

Avoidance of intense midday sun and its associated heat loads appears to be important to Mallards and teal, but exploitation of the sun's energy also may be important, especially for the smaller-sized teal. Because of their small size, teal rely primarily on food to meet the costs of incubation, whereas Mallards rely to a greater extent on endogenous reserves (see Afton and Paulus 1992). Therefore, teal may be

more responsive to alternate energy sources than are Mallards. Indeed, teal nest sites received greater insolation and experienced higher T_c than did Mallard nest sites.

Although exploitation of insolation to offset metabolic costs may be advantageous, it must be balanced against risks of overheating of eggs and females. These risks may be especially important at nests that are too exposed. At high temperatures, small-bodied teal may accumulate significant heat loads, potentially resulting in increased recess frequency as females attempt to lower body temperature and replenish water lost through transpiration. As recess frequency increases, nests could become more vulnerable to detection by visually foraging predators (Erikstad et al. 1982). Furthermore, eggs left unattended may reach lethal temperatures.

Use of insolation as an additional energy source for incubating birds may account for the relatively narrow range of habitats used by nesting teal (Gloutney 1996). Factors other than microclimate may be more important determinants of nest-site selection by Mallards because they are able to commence egg laying earlier than teal (Greenwood et al. 1995, Gloutney 1996). Additionally, Mallards often nest in cool, shady aspen groves, suggesting that nest-site selection is not based on use of supplemental heat, at least for some females (Gloutney 1996).

Differences in T_c originate in part from interspecific differences in thermal resistance, which in turn arise at least partly from size differences between teal and Mallards. Effects of size are manifested through different areas receiving insolation as well as a physical constraint imposed by surface-area-to-volume ratios. The plumage of these species also has different heat-transfer coefficients (Mallards: $0.8 \pm 0.12 \text{ W/m}^2\text{C}^{-1}$; teal: $0.92 \pm 0.1 \text{ W/m}^2\text{C}^{-1}$; Brown 1985). Size and insulation characteristics result in teal losing heat at a greater rate than Mallards, which may account in part for later nesting and selection of relatively warm nest sites by teal.

The MSH predicts that microclimatic conditions should vary less at nest sites than at adjacent sites. However, for both species, the coefficients of variation for microclimatic variables did not differ between nest sites and adjacent sites. Furthermore, our results did not

support the prediction that teal should nest in a more restricted range of microclimatic conditions because there were no interspecific differences in variance for any of the microclimatic variables. Much of the inherent variability is due to daily variation in ambient conditions, possibly precluding females from selecting sites with reduced variability. Therefore, fine-scale reduction in nest microclimate variability may be masked by large-scale variation in ambient conditions. Response to ambient conditions, therefore, should occur at the scale of timing of breeding (Hammond and Johnson 1984).

Predation pressure influences the evolution of many life-history strategies, including nest-site selection. High incidences of nest predation should drive selection for less vulnerable nest sites (e.g. Holway 1991, Li and Martin 1991, Tuomenpuro 1991, Martin 1995). However, Filiater et al. (1994) argued that a rich assemblage of nest predators may eliminate predictably safe nest sites because a safe site with respect to one predator may be a vulnerable site to a different predator. Additionally, Clark and Nudds (1991) reported that successful and unsuccessful ground nests could not be distinguished on the basis of concealment alone except when birds were the dominant predators. Because Mallards and teal were subjected to a diverse predator assemblage in our study area (R. G. Clark unpubl. data), most females may have been unable to find predictably safe nest sites. If microclimate considerations were important for fine-tuning nest-site choices, we were unable to detect which variables influenced these choices.

In order to hatch successfully, eggs must experience appropriate water loss during incubation (Ar and Rahn 1980). Regardless of shell conductance, water loss in eggs is determined by the inherent behavior of birds in terms of nesting season, microclimate, and nest structure, all of which keep nest humidity relatively constant (Ar 1993, Rahn 1993). However, birds do not actively regulate nest water-vapor pressure during incubation (Walsberg 1983b, Rahn 1984, Kern et al. 1990). Because we monitored RH outside of the nest, we probably underestimated the influence of RH on evaporative heat loss of incubating females. Weathers (1979) found that high ambient humidity reduces effectiveness of evaporative cooling as a mecha-

nism for dissipating heat loads. We found no evidence that nest sites had lower humidity than adjacent sites.

Temperature and embryonic development.—Birds should adopt incubation strategies that minimize the amount of time eggs are exposed to temperatures below the physiological zero temperature (PZT; 25°C). In 14 species of passerines, parents adopted an incubation strategy of returning to the nest before their eggs reached PZT (Haftorn 1988). Unattended eggs cool at a rate that depends on thermal gradients between eggs and the environment (Turner 1985, 1993). During incubation recesses, egg and nest temperatures converge (Turner 1993). Therefore, with respect to egg cooling, the optimal time to leave the nest is when nest temperatures correspond to typical egg temperatures during incubation (38°C). However, nest-site temperatures rarely were this high. One way birds could minimize exposure of eggs to temperatures below 25°C would be to take recesses when nest temperatures are above 25°C. If this is true, then Mallards and teal should leave their nests between 1100 to 1800 and 1030 to 1800, respectively (Fig. 3). However, Mallards, and to a lesser extent teal, typically were away from their nests between 1800 to 2100 (Gloutney et al. 1993), suggesting that other considerations were more important determinants of patterns of nest attendance. For example, patterns of recess initiation may be linked to predator activity or diurnal patterns of food availability. Further work is needed to evaluate the consequences of microclimate selection on embryonic temperature and development.

Assessment of operative temperature calculations.—The mean values of T_e were relatively high during the afternoon (maximum at nest = 41.4°C for Mallard, 55.5°C for teal), when nest-site temperature and insolation were highest. T_e values were not unrealistic compared with other studies. For example, standard operative temperature for perching Phainopeplas (*Phainopepla nitens*) may be as high as 55°C (Walsberg 1993).

A problem in the calculation of T_e arises in determining area of the bird receiving short- and longwave radiation, because area is influenced both by posture and orientation to the sun (Walsberg 1992). We assumed a constant orientation (perpendicular to the sun) and pos-

ture, but live birds may alter their posture and orientation to receive solar insolation during cold periods or to avoid it during hot periods (Bartholomew and Dawson 1979, Lustick et al. 1980). We were unable to include behavioral responses such as ptiloerection, which decreases plumage conductance but increases plumage conductivity (Hill et al. 1980). Further, orientation perpendicular to the sun results in maximum surface area exposed to insolation. Therefore, reported values probably represent maximum thermal conditions for ducks.

Shelter from wind can affect total energy demands of roosting birds (e.g. Walsberg 1986, Webb and Rogers 1988, Jenni 1991, With and Webb 1993; but see Walsberg and King 1980). However, wind speeds often are negligible at ground level. In fact, calculated wind speeds at nest sites and adjacent sites were less than 0.25 m/s, and low wind velocities at nests have been reported for ground-nesting passerines (With and Webb 1993). Air flow has a substantial effect on T_e because total thermal and body resistance are closely correlated with the square root of wind velocity (Walsberg 1986, Bakken 1992). For example, Stahel et al. (1987) found that thermal resistance decreased with increasing wind speed in the Little Penguin (*Eudyptula minor*), whereas field metabolic rates of Doves (*Alle alle*) were influenced only by wind (Gabrielsen et al. 1991). Thus, it is not surprising that ground nests within vegetation experience relatively little convective heat loss, and consequently, exhibit relatively high T_e . Because calculation of resistance for convective heat flow (r_a ; see Appendix) assumes that animals are in a forced convective environment, our estimates of r_a may be biased upwards, resulting in high T_e values.

In summary, Mallards and Blue-winged Teal appear to select nest sites that provide concealment from midday sun, which would reduce potential heat stress to incubating females. Our results provide only limited support for the MSH, with Mallard nest sites receiving more insolation and experiencing greater T_e relative to adjacent sites. Contrary to predictions, duck nest sites and their adjacent sites did not differ in: (1) variability of microclimatic conditions, (2) temperature, and (3) relative humidity. Furthermore, teal selected warmer nest sites than Mallards. Nest-site selection undoubtedly represents a tradeoff be-

tween a number of competing constraints, such as microclimate and predation risk (Gloutney 1996). Quantification of these constraints is necessary to establish the extent of their influence on nest-site selection in ducks. Within suitable nesting habitats, chance events may exert a greater influence on nest fate than do the characteristics of females or their nests. If this is true, then we would expect that nest sites and random sites would differ little with respect to vegetational and microclimatic characteristics. Finally, we suggest that differences in nest locations among duck species are due in part to differential importance of environmental heat as an energy source to meet the energetic costs of incubation, but this hypothesis is untested.

ACKNOWLEDGMENTS

We thank all the students involved with data collection, G. Walsberg for advice on calculating operative temperature, K. Beal for advice on repeated measures analyses, and K. Guyn, K. Hobson, and D. Shutler for helpful comments on the manuscript. Comments by Stuart Paulus and two anonymous reviewers improved the manuscript. We gratefully acknowledge financial support of the Canadian Wildlife Service, postgraduate scholarships to M.L.G. from the University of Saskatchewan and the Natural Sciences and Engineering Research Council of Canada (NSERC), and a research grant to R.G.C. from NSERC. The study was approved by the University of Saskatchewan's Animal Care Committee (Protocol 910224) on behalf of the Canadian Council on Animal Care.

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APPENDIX. Calculation of operative temperature.

Operative temperature (T_e) was calculated as follows (Walsberg and King 1978):

$$T_e = T_g + (R_{abs} - \epsilon \sigma T_a^4) / (\rho c_p), \tag{1}$$

where T_g is temperature at ground level at random sites (measured as 30-min means), R_{abs} is radiation absorbed by the duck, ϵ is surface emissivity, σ is the Stephan Boltzmann constant, r_e is the parallel equivalence resistance, and ρc_p is a constant. R_{abs} was calculated after Mahoney and King (1977):

$$R_{abs} = (SW_p \cdot A_p / A_i \cdot \alpha_{sw}) + (LW_p \cdot A_p / A_i \cdot \alpha_{lw}), \tag{2}$$

where SW_p is shortwave radiation, LW_p is longwave radiation, A_p is area of the bird receiving short- or longwave radiation, A_i is the total area of the bird potentially receiving radiation (i.e. above the nest), and α_{sw} and α_{lw} are absorptivities to short- and longwave radiation, respectively. SW_p is shortwave radiation measured as 30-min means. Problems associated with obtaining A_p/A_i include posture and orientation, as well as temporal changes in solar position/elevation. To standardize effects of these factors, we assumed that birds maintained a constant posture and orientation to the sun, with the long axis of the bird being perpendicular to the sun. Solar elevations change temporally and seasonally. Solar elevations were adjusted following Walsberg (1992). Solar elevation (ϕ) was calculated for each 30-min period of each day when nests were monitored according to Walsberg (1992):

$$\phi = \sin^{-1} [\sin \Gamma \sin \delta + \cos \delta \cos \Gamma \cos (15 [t - t_N])], \tag{3}$$

where Γ is latitude, δ is solar declination angle, t is current time, and t_N is time of local solar noon. δ and t_N were estimated following Walsberg (1992):

$$\delta = -23.45 \cos (0.986 D + 8.87), \tag{4}$$

where D = Julian date and angles are in degrees; and

$$t_N = 12 + (L_l - L_c) / 15 + C, \tag{5}$$

where, L_l is local latitude, L_c is the central meridian of local time zone (to nearest even multiple of 15°). Additionally, a correction factor C is required to account for variation in angular velocity of the earth's rotation during the annual cycle. Values of C were estimated from Walsberg (1992):

$$C = (-0.12 \sin[0.986D]) - (0.16 \sin[1.973D]) - (0.05 \cos[1.973D]). \tag{6}$$

To determine the amount of solar radiation that would be received by incubating ducks, we measured surface areas of Mallards and Blue-winged Teal using carcasses frozen into an incubation posture. Each bird was wrapped in thin commercial plastic wrap. A light was shone on the bird in a dark room at angles from 10 to 70°, in 10° intervals, and

the area intercepting light was outlined. Traces were subsequently digitized to determine area. Total area of the bird potentially receiving radiation was measured using the same procedure. A_p/A_i was then calculated for each angle and species, and the values were used to develop the following polynomial regressions for the relationship between A_p/A_i and ϕ :

Mallard ($R^2 = 0.946$):

$$A_p/A_i = 0.0416 + 0.0139\phi - 0.00012\phi^2, \tag{7}$$

and

Blue-winged Teal ($R^2 = 0.952$):

$$A_p/A_i = 0.0549 + 0.0205\phi - 0.00019\phi^2. \tag{8}$$

The absorptivity of plumage to shortwave radiation was unavailable for ducks. Consequently, we estimated α_{sw} based on solar reflectance (SR) for Northern Bobwhites (*Colinus virginianus*) and Eastern Meadowlarks (*Sturnella magna*), whose plumage is similar in color to that of Mallards and Blue-winged Teal. Calder and King (1974) reported SR = 0.22 for bobwhites and meadowlarks. Accordingly, from the relationship $\alpha_{sw} = 1 - SR$, we used $\alpha_{sw} = 0.78$ for the ducks.

Longwave radiation incident on the bird was not measured, so it was estimated from the Stephan Boltzmann Law (Campbell 1977) because we had data on ambient temperature (T_a) and relative humidity 1.5 m above ground level.

$$\Phi_B = \epsilon \sigma T_a^4, \tag{9}$$

where Φ_B is emitted flux density in W/m^2 , $\sigma = 5.67 \times 10^{-8} W/m^2 K^4$, and T_a is temperature in °K. ϵ was estimated as:

$$\epsilon = 0.72 + 0.005 \cdot T_a. \tag{10}$$

In this way, we estimated surface temperature of vegetation near each site. We used the same estimate of longwave radiation as we used for shortwave radiation. Absorptivity to longwave radiation was unavailable for waterfowl. Thus, we assumed it was 0.98 based on Calder and King's (1974) value for Willow Ptarmigan (*Lagopus lagopus*), which are similar in color to Mallards and Blue-winged Teal.

The parallel equivalent resistance of the boundary layer, r_w was calculated after Mahoney and King (1977):

$$1/r_e = 1/r_a + 1/r_r = (r_a \cdot r_r) / (r_a + r_r), \tag{11}$$

where r_a is the resistance to convective heat flow:

$$r_a = k(d/u)^{0.5}, \tag{12}$$

r_r is an apparent radiative resistance:

$$r_r = \rho c_p / 4\epsilon \sigma T_g^3, \tag{13}$$

$k = 215$ (for outdoor conditions with non-laminar flow; Walsberg and King 1978), d is the diameter of birds perpendicular to the plane of solar insolation (0.24 m for Mallards and 0.20 m for Blue-winged Teal), and $\rho c_p = 1,200 J/m^3 \cdot K^{-1}$.

Wind speed (u) was measured in m/s within 60 m of each site. From this, we calculated wind speed 4 cm above the ground with the formula of Campbell (1977):

$$u = u^*/k \ln ((z + z_m - d)/ z_m), \quad (14)$$

where u^* = friction velocity, k is the Von Korman constant (0.4), z is the measurement height of 0.04 m, and $z_m = 0.13 \cdot (\text{mean canopy height})$; z_m corresponds to the height where wind speed = 0 and $d = 0.64 \cdot (\text{mean canopy height})$, which corresponds to zero plane displacement.