

WETLAND SELECTION BY MALLARDS AND BLUE-WINGED TEAL

JOHN H. MULHERN, THOMAS D. NUDDS, AND B. RICHARD NEAL

A precursor to the question of which environmental and physiological factors influence habitat choice is the question of whether organisms *select* (defined here as exhibiting a preference) habitat at all, and if so, what constitutes evidence of habitat preference. Hildén (1965) suggested that birds choose the best available habitat. It does not follow, however, that the observed distributions of organisms are the result of habitat preference, because birds may be constrained in their choice of habitat by geophysical events and the effects of interactions within and among species (Partridge 1978).

Habitat use by breeding ducks often has been studied (e.g., Evans et al. 1952, Evans and Black 1956, Bengston 1971, Smith 1971, Stoudt 1971, Dwyer et al. 1979, Wheeler and March 1979) with the implicit or explicit purpose of delineating "critical habitats." Biologists have attempted to determine habitat preferences of ducks by correlating duck densities with environmental variables (e.g., Lokemoen 1973, Stewart and Kantrud 1974, Weller 1979, Joyner 1980, Godin and Joyner 1981). From these types of analyses, it is usually concluded that the "preferred" habitats are those with an abundance of the habitat features correlated with duck density.

Here, we present results of a multivariate analysis of selection of structurally different wetlands by breeding Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*). Our objectives were (1) to test whether Mallards and Blue-winged Teal exhibit habitat selection as evidenced by disproportionate use of habitats, (2) to examine whether there is interspecies variation in the tendency for each species to select habitats, and (3) to test whether breadth of habitat use is related to density of birds.

STUDY AREA AND METHODS

The study was conducted from late April to mid-August, 1977 to 1980, on 388.5 ha of aspen parkland approximately 47 km east of Saskatoon, Saskatchewan. Complete descriptions of the area can be found in Sugden (1977). Ninety-eight wetland basins were present on the study area, but the number with standing water varied annually and seasonally.

Duck censuses.—Five censuses were conducted at 10-day intervals from late April to mid-June each year, except in 1979 when a late spring delayed surveys for approximately 10 days.

Counts were conducted on all ponds by walking through the area, except where wetlands were close to roads and observable from a vehicle. All Mallard and Blue-winged Teal pairs, lone drakes, lone hens, and groups of drakes were recorded. Total males and females were

noted and discernible pairs within flocks of the same species were recorded. All counts were conducted between 08:00 and 12:00 h when pairs and drakes were least mobile (Diem and Lu 1960, Dzubin 1969). Censuses were not made during periods of rain or high winds, but they were continued during periods of cloud cover. An effort was made not to disturb the ducks during counts so as to minimize the risk of counting them twice. Two investigators worked together, enabling one to determine the destination of birds that flushed and to adjust counts accordingly.

Brood surveys were conducted, at approximately 15-day intervals, from late June to mid-August. Either five (1977) or four (1978–80) surveys were conducted annually during early morning and late evening when broods were feeding and most visible (Ringelman and Flake 1980). All observations were used in the analyses of habitat selection.

Brood production on the study area was estimated initially using the method developed by Gollop and Marshall (1954). This estimate was modified by including broods whose age class indicated they were present on previous surveys, but not seen and recorded. We then assumed that breeding pair density was related to brood production. To determine which of the birds present on the study area during the breeding period could be designated members of breeding pairs, the brood production of each species was regressed against four different breeding pair densities: total ducks, observed pairs, observed pairs plus single males, and observed pairs plus males in groups of five or less. The index that accounted for the most variation in the number of broods was selected as the best estimate of breeding pairs, and all observations of adult birds so designated were used in analyses of habitat selection.

Habitat measurements.—Pond size and several features of emergent and upland vegetation immediately surrounding the ponds were recorded during each census. The percentage of the pond surface covered by emergent vegetation was assigned to one of five categories (0–10%, 11–25%, 26–50%, 51–75%, and >75%). Vegetation height was assigned to one of five classes (0–0.25 m, open water and low mat vegetation; 0.25–0.50 m, wet meadow vegetation; 0.5–1.0 m, sedge [*Carex* sp.] and white-top grass [*Scholochloa festuacaea*]; 1.0–2.0 m, cattail [*Typha latifolia*]; and 2.0 m, shrubs and trees). Interspersion of emergent vegetation and water was assigned to one of three classes: uniform, partially interspersed, or heavily interspersed (after Stewart and Kantrud 1971). Trees and shrubs were coded as not present, partially surrounding, or completely surrounding the ponds. The structure of vegetation was coded by classes of vegetation stature: low (summer-fallow fields), intermediate (native grasses), and tall (cereal crops).

Statistical methods.—To distinguish between proportionate (non-selective) and disproportionate (selective) use of available wetlands, we constructed three models of habitat use in relation to habitat availability (Fig. 1). If there was no statistical difference between the structural distributions of wetlands available and the structural distributions of wetlands used by ducks (Model A) (Fig. 1), we rejected the hypothesis that the ducks selected wetlands (i.e., habitat use simply “mapped” to habitat availability). When the ponds used by ducks differed from those available, however, it may have been due either to changing such habitat preferences relative to varying habitat availability (Model B) (Fig. 1), or to stenotopic habitat use despite varying habitat availability (Model C) (Fig. 1). In drought years, for example, only deep, large, permanent ponds are generally available; in other years, a wide assortment of ponds, both shallow and small, and deep and large, is available. To test among these alternatives, we used data on habitat use by Mallard and Blue-winged Teal breeding pairs and hens with broods in two structural habitat dimensions constructed from principal components analysis (PCA; Nie et al. 1970).

Data analysis.—Three sets of principal component (PC) scores were used to characterize wetland habitat. Two of these sets described the structure of all wetlands in the study area during breeding and brood-rearing. These are referred to as the “May ponds” (all wetland

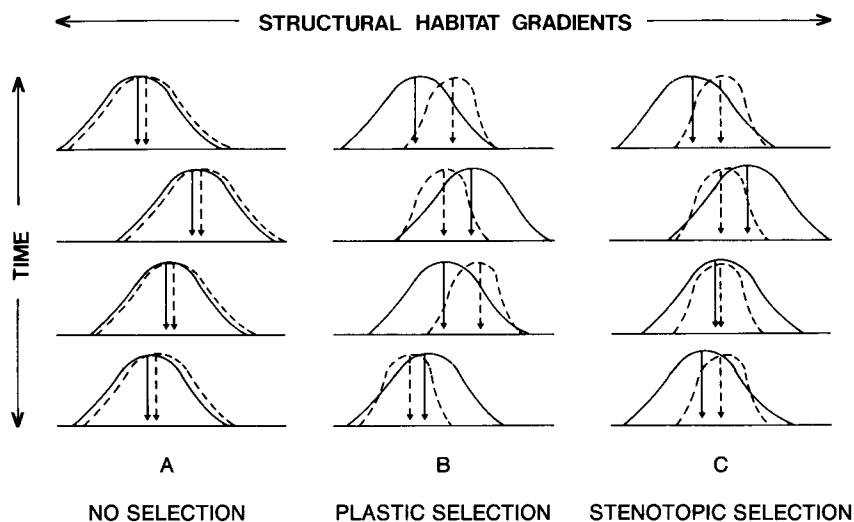


FIG. 1. Three models of habitat use (— — —) in relation to habitat availability (—) representing variation over four time units. In each model, temporal variation in habitat availability is the same, but difference in habitat use patterns can result in three types of habitat "selection." A = No selection: habitats used "map to" those available. B = "Plastic" habitat selection: habitats used are statistically different from those available but not temporally consistent. C = "Stenotopic" habitat selection: habitats used are statistically different from those available and consistent through time, despite variation in available habitats.

basins containing water on the first census of breeding pairs) and the "July ponds" (all basins containing water during the first brood census after shallow, ephemeral wetlands dried up). The third set of principal component scores described the structure of all wetlands used by ducks during breeding and brood-rearing (i.e., subsets of "May ponds" and "July ponds"). These are referred to as "Duck ponds." The component scores of wetlands used by pairs were compared with the component scores of the wetlands available during May; the component scores of the wetlands used by broods were compared with the component scores of those available in July.

Between-year variation in wetland availability due to the annual variability in wetness regimes presented a problem when attempts were made to distinguish among the alternative types of habitat use displayed in Fig. 1. In particular, due to the presence and absence of different structural types of wetlands in "wet" and "dry" years, different habitat variables might have contributed differentially to the construction of the principal components from year to year. We pooled data across years within each data set to make the resultant principal component scores all relative to long-term average habitat conditions, thereby facilitating comparison of PC scores among years on a common scale (Nudds 1983).

The variable loadings on the first principal component for May ponds were compared with the loadings on the first principal component for Duck ponds, loadings on the second principal component for May ponds were compared with loadings on the second principal component for Duck ponds, etc. (Rotenberry and Wiens 1980:1242-1243, Landres and MacMahon 1983:186) with Spearman ranked order correlation. Nonparametric correlations

were used because the distribution of variable loadings was unknown and because degrees of freedom was small ($N = 6$ variable loadings). If the correlations were significant, we declared the axes derived from each principal component analysis sufficiently similar to warrant direct comparison of the distributions of scores on those axes. If the ranked order correlations were insignificant, we declared the habitats used different from those available (i.e., selection occurred) and that inspection of the variable loadings would yield information about how the wetlands used differed from those available.

If the ranked order correlations were significant, we compared variation in principal component scores between wetlands used and wetlands available in two ways to determine if the wetlands used by pairs and hens with broods of either species differed in any year from those available (Model A vs Model B or C) (Fig. 1). First, Student's *t*-tests were used to test for differences in mean location of birds in structural habitat space with the mean location of habitats available in that space. Second, we compared the variance in structural habitats used by birds with the variance in the habitats available. Significant differences in the mean of characteristics of those wetlands used vs those available, or significantly narrower variance in wetlands used vs those available, were considered evidence of habitat selection.

We were liberal at setting rejection levels for the null hypothesis of no habitat selection because comparing a distribution that is a subset of another tends to increase the chance of committing a Type II error. On the other hand, the replication of observations on the same breeding pairs of each species implies a lack of independence among observations which would tend to increase the chance of committing a Type I error. We chose $\alpha = 0.10$ in analyses of both pairs and broods as a compromise rejection level.

If birds were found to be selecting habitats, we used ANOVA to compare the magnitude of the among-year variation in the structure of used and available wetlands, thereby distinguishing between stenotopic and plastic selection (Model B vs Model C) (Fig. 1). If among-year variation in wetlands used was greater than among-year variation in wetlands available, then habitat selection was plastic (Model B). If, however, the distributions of wetlands used varied less through time than did the distribution of wetlands available, then habitat selection was relatively consistent even though habitat available changed from year to year (Model C).

RESULTS

Breeding pair abundance. — Observed pairs plus males in groups of five or less accounted for the most variance in brood abundance for both Mallards and Blue-winged Teal (Table 1). For Mallards, this index was significant ($P < 0.05$), but for Blue-winged Teal it was not. Therefore, the total of observed pairs plus males in groups of five or less was also used as the best estimate of Blue-winged Teal breeding pairs. This finding is consistent with those of other studies; Hammond (1969), Wheeler and March (1979), and Ruwaldt et al. (1979) used this index of breeding pairs for dabbling ducks. Hereafter, breeding pairs, or simply pairs, refers to observed pairs plus males in groups of five or less. All individuals so recorded comprised the sample of ducks on which the determination of wetland use by breeding pairs was based. Sample sizes for analyses of habitat selection by pairs and hens with broods are given in Table 2.

Comparison of principal component loadings for different data sets. — In all data sets, wetlands were arrayed along the first principal axis from open ponds with low vegetation to closed ponds with tall emergent vege-

TABLE 1
REGRESSION STATISTICS (SLOPE AND *t*-TEST OF ITS DIFFERENCE FROM ZERO) OF VARIOUS
INDICES OF BREEDING PAIR ABUNDANCE AND BROOD ABUNDANCE

Indices of pair abundance	Mallard		Blue-winged Teal	
	Slope	<i>t</i> ₁₈	Slope	<i>t</i> ₁₈
Total ducks	0.45	2.19 ^a	0.20	0.89
Observed pairs	0.08	0.38	0.19	0.83
Observed pairs plus single males	0.09	-0.39	0.26	1.15
Observed pairs and groups of five males or less	0.46	2.25 ^a	0.28	1.26

^a $P < 0.05$.

tation. The second principal axis denoted a gradient of increasing pond size and vegetation interspersion (Table 3). The structures of the same principal components from each data set were similar (Table 4).

Habitat use by ducks.—There were no differences between the distributions of wetlands used by Mallard pairs and the distributions of wetlands available in May ($P > 0.10$) (Table 5). Neither did Mallard pairs use a narrower range of wetlands than those available. Thus, we could not detect wetland selection by Mallard pairs, and they appeared to use structurally different wetlands in proportion to their availability.

Three of eight *t*-tests between component scores of May wetlands and those wetlands used by pairs of Blue-winged Teal were significant ($P < 0.05$) (Table 5). In 1977, on PC1, pairs of Blue-winged Teal chose closed ponds characterized by tall vegetation. In 1978, on PC2, pairs of Blue-winged Teal selected large ponds interspersed with emergent vegetation, but in 1979, on PC2, they selected small ponds with uniform vegetation. In addition, pairs of Blue-winged Teal used a narrower range of wetlands than was available on PC1 in 1978.

Mallard broods showed some evidence of habitat preference but, in general, used wetlands in proportion to their availability. The only differences between wetlands used by Mallard broods and the wetlands available in July were in 1977 and 1979 (Table 6) when Mallard broods, on PC2, selected large wetlands interspersed with vegetation. These were the two years when there were few Mallard broods (Table 2). In 1978, Mallard broods used a narrower range of wetlands than was available on PC1.

Four of eight *t*-tests between component scores of July wetlands and component scores of wetlands used by broods of Blue-winged Teal were significant (Table 6). In 1979 and 1980, on PC1, they selected open ponds characterized by low vegetation. In 1977 and 1978, they used a narrower range of wetlands than was available on PC1. In 1977 and 1978, on PC2,

TABLE 2
SAMPLE SIZES USED IN THE ANALYSES OF HABITAT SELECTION BY MALLARD AND
BLUE-WINGED TEAL PAIRS AND HENS WITH BROODS

Year	Number of wetlands		Breeding pairs ^a		Broods	
	May	July	Mallard	Teal	Mallard	Teal
1977	66	46	228	238	6	35
1978	82	33	219	124	15	21
1979	98	66	129	98	8	21
1980	90	40	282	136	21	26
Total	336	185	868	596	50	103

^a Breeding pairs include observed pairs and males in groups of five or less. Figures are totals of five censuses in each year. Because broods are relatively sedentary, although pairs move from wetland to wetland, brood abundance is an estimate of the minimum number of broods present; breeding pairs is the total number of observations of pairs.

broods of Blue-winged Teal chose large ponds interspersed with emergent vegetation. These same trends were evident in 1979 and 1980, but were not significant; however, in 1979 teal used a significantly narrower range of wetlands than was available on PC2. These patterns bore no relationship to density of broods of Blue-winged Teal (Table 2).

Pairs and broods of Mallards generally exhibited Model A (Fig. 1) habitat use. Blue-winged Teal pairs, however, varied more in their selection of wetlands than did wetland availability in either habitat dimension (Table 7); thus they followed Model B (Fig. 1) habitat selection. Conversely, teal broods were relatively stenotopic in their selection of wetlands (Model C) (Fig. 1) in the first habitat dimension, but plastic (Model B) in their selection of wetlands in the second habitat dimension (Table 7).

DISCUSSION

Pairs of breeding Mallards were not selective but generally used structurally different wetlands in proportion to their availability. Other studies have reported a similar lack of preference for breeding habitat by Mallards. For example, Dwyer et al. (1979) studied the use of prairie potholes by Mallards in south-central North Dakota and concluded that there were no preferences in the use of different wetlands. Patterson (1976) studied Mallard use of heterogeneous beaver ponds in Ontario and found that pairs were evenly distributed over all ponds. In contrast, Gilmer et al. (1975) studied habitat use by Mallards in the forested region of north-central Minnesota and found that they preferred seasonal wetlands, sand-bar ponds, and overhanging brush shorelines, although they recognized this species was ubiquitous and capable of utilizing a wide variety of habitats.

Pairs of Blue-winged Teal used wetlands disproportionately in three of

TABLE 3
FACTOR LOADINGS AND AMOUNT OF VARIANCE ACCOUNTED FOR BY PCA RUN ON MAY PONDS, JULY PONDS, AND DUCK PONDS

Variables	May ponds		July ponds		Duck ponds	
	PC1	PC2	PC1	PC2	PC1	PC2
Pond size	-0.13	0.82	-0.29	0.80	-0.31	0.83
Vegetative cover	0.75	-0.32	0.83	-0.06	0.76	-0.12
Vegetation height	0.80	-0.05	0.68	0.29	0.58	0.33
Interspersion of vegetation	0.09	0.68	0.12	0.77	0.18	0.79
Structure of peripheral vegetation	0.57	0.36	0.50	-0.01	0.68	0.05
Upland vegetation	0.39	0.10	0.14	0.00	0.45	-0.04
Cumulative variance accounted for	53.3%		48.1%		53.5%	

four years, but the structure of wetlands they chose varied annually. Reasons for this inconsistency in habitat selection are not apparent; teal might have cued on some habitat features not measured and uncorrelated with any of the features included in these analyses. Pond fertility, available food resources, water depth, and amount of submergent vegetation were not measured and may have been important to birds in the selection of wetlands (Ringelman and Longcore 1982, Talent *et al.* 1982). Structural habitat features, such as we measured, however, appear to act as proximate cues to food-rich areas (e.g., Kaminski and Prince 1981, Murkin *et al.* 1982) so it is not clear whether the omission of data on submerged vegetation and food density would substantially alter our conclusions. Habitat selection by Blue-winged Teal has been demonstrated elsewhere. Stewart and Kantrud (1973) found a disproportionate number of pairs of Blue-winged Teal on shallow seasonal wetlands in the prairie pothole region of North Dakota. Fifty-two percent of all Blue-winged Teal were found on seasonal wetlands, yet seasonal wetlands represented only 21% of the available habitat. In a second study, Stewart and Kantrud (1974) found yearly variations in abundance of Blue-winged Teal were correlated with the abundance of seasonal wetlands. Evans and Black (1956) reported that pairs of Blue-winged Teal preferred large wetlands early in the breeding season. Dispersion to smaller wetlands did not occur until May when numbers of pairs increased and larger wetlands appeared crowded. Blue-winged Teal showed a preference for larger wetlands at our study site in 1978. Perhaps there were sufficient large wetlands to accommodate Blue-winged Teal in 1978 and dispersion to smaller wetlands did not occur.

TABLE 4
 SPEARMAN RANK CORRELATION (N = 6 VARIABLES) BETWEEN VARIABLE LOADINGS ON PRINCIPAL COMPONENTS DESCRIBING DUCK PONDS WITH EACH OF MAY PONDS AND JULY PONDS

Component scores correlated	Principal component 1		Principal component 2	
	r_s	P	r_s	P
Wetlands used by pairs with wetlands available in May	0.82	0.021	0.82	0.021
Wetlands used by broods with wetlands available in July	0.94	0.002	0.94	0.002

With the exception of 1977 and 1979, when Mallard broods chose large wetlands interspersed with vegetation, and 1978, when they selected wetlands with intermediate vegetative cover, Mallards used wetlands in proportion to their availability. In contrast, Evans et al. (1952) found that Mallard broods used small potholes but were still the most widely distributed species. As in our study, Bengston (1971) and Courcelles and Bédard (1979) found that Mallard broods used ponds containing emergent vegetation. This may have been related to the availability of invertebrates (Talent et al. 1982), which are more common in vegetated ponds than those lacking vegetation (Krull 1970), and are important foods of duck-

TABLE 5
 RESULTS OF *t*-TESTS AND *F*-TESTS ON PRINCIPAL COMPONENT SCORES OF MAY PONDS USED BY MALLARD AND BLUE-WINGED TEAL PAIRS

Year	May ponds		Mallard				Blue-winged Teal			
	\bar{x}	s^2	\bar{x}	s^2	P^{*a}	P^{*b}	\bar{x}	s^2	P^*	P^b
PC1										
1977	-0.11	0.81	0.07	0.82	NS	NS	0.31	0.83	0.001	NS
1978	-0.12	1.14	-0.20	0.87	NS	NS	-0.30	0.66	NS	0.007
1979	0.03	1.10	0.11	0.90	NS	NS	-0.03	1.15	NS	NS
1980	0.16	0.89	0.01	1.43	NS	NS	0.18	1.19	NS	NS
PC2										
1977	0.39	1.07	0.21	1.16	NS	NS	0.15	1.09	NS	NS
1978	-0.10	0.86	-0.16	0.78	NS	NS	0.45	1.11	0.001	NS
1979	-0.96	1.03	-0.24	0.82	NS	NS	-0.37	0.76	0.045	NS
1980	-0.09	0.95	-0.23	0.81	NS	NS	-0.26	1.03	NS	NS

^a P^* is the probability of a two-tailed pairwise *t*-test adjusted, if necessary, for unequal variances.

^b P^b is the probability of a one-tailed *F*-test for equality of variances.

TABLE 6
RESULTS OF *t*-TESTS AND *F*-TESTS ON COMPONENT SCORES OF JULY PONDS USED BY MALLARD AND BLUE-WINGED TEAL BROODS

Year	July ponds		Mallard				Blue-winged Teal			
	\bar{x}	s^2	\bar{x}	s^2	P^a	P^{b*}	\bar{x}	s^2	P^a	P^{b*}
PC1										
1977	-0.45	0.91	-0.11	0.66	NS	NS	-0.20	0.22	NS	0.001
1978	-0.15	1.30	0.25	0.27	NS	0.003	-0.43	0.59	NS	0.001
1979	0.29	0.73	-0.06	1.05	NS	NS	-0.22	0.44	0.01	NS
1980	0.16	0.93	-0.27	2.14	NS	NS	-0.43	0.55	0.01	NS
PC2										
1977	0.15	1.03	1.20	0.49	0.01	NS	0.78	0.88	0.01	NS
1978	-0.00	0.96	0.23	0.49	NS	NS	0.68	1.03	0.01	NS
1979	-0.15	1.00	0.54	0.78	0.06	NS	0.02	0.23	NS	0.001
1980	0.08	0.99	-0.03	0.41	NS	NS	0.29	0.72	NS	NS

^a P^a is the probability of a two-tailed pairwise *t*-test adjusted, if necessary, for unequal variances.

^b P^{b*} is the probability of a one-tailed *F*-test for equality of variances.

lings (Chura 1961, Collias and Collias 1963, Perret 1962, Sugden 1973, Driver et al. 1974).

Broods of Blue-winged Teal showed stenotopic selection for open wetlands characterized by little vegetation. Stoudt (1971), Lokemoen (1973), and Mack and Flake (1980) also found that broods of Blue-winged Teal used open wetlands and relied on open water and diving for escape. Evans et al. (1952) and Courcelles and Bédard (1979), however, found that teal broods were associated with emergent vegetation. In 1977 and 1978, we also found that broods of Blue-winged Teal disproportionately used large wetlands with interspersed vegetation, but they were more plastic in their

TABLE 7
ANOVA TESTS FOR VARIABILITY IN HABITAT USE BY BLUE-WINGED TEAL PAIRS AND BROODS VERSUS VARIABILITY IN HABITAT AVAILABILITY IN MAY AND JULY

Period	Habitat dimension	<i>F</i>	<i>P</i>	Population component	<i>F</i>	<i>P</i>
May	PC1	1.5	0.22	Pairs	11.8	0.0001
	PC2	4.2	0.006	Pairs	17.2	0.0001
July	PC1	6.2	0.0005	Broods	1.13	0.34
	PC2	1.04	0.38	Broods	4.19	0.008

selection of wetlands in that habitat dimension than in the other (see also Weller 1979).

One prominent hypothesis about habitat selection is that only the best habitats are used when the number of animals in a population is low (Hildén 1965, Fretwell and Lucas 1969, Partridge 1978). The pattern of selection in the first habitat dimension by Blue-winged Teal hens with broods in 1979 seems to support the hypothesis, because one would expect habitat preferences to be most evident in 1979 when a large number of ponds was available for the lower than average number of broods (Table 2); however, selection was evident in at least one dimension in all of the other years as well (Table 6). The pattern of selection by Mallard broods may also be consistent with the hypothesis. Selection was evident in 1977 and 1979 (Table 6), i.e., in those years when wetland numbers were high and brood density was low (Table 2). Similarly, Talent et al. (1982) found evidence of disproportionate use of some wetlands by Mallard broods when wetlands were abundant, but habitat use conformed to habitat availability when wetlands were more scarce.

We conclude that both Mallards and teal select wetlands, particularly during brood-rearing, but that wetland use most often conforms to wetland availability. The dynamic nature of wetland habitats, and the corresponding spatial and temporal variation in the requisites for successful breeding by waterfowl, appear to have selected for plastic habitat-use strategies by ducks. Consequently, different components of entire wetland complexes might all be important at different times during the breeding period (Patterson 1976, Swanson et al. 1979, Duebbert and Frank 1984).

SUMMARY

Four years of observations of habitat use by breeding pairs and broods of Mallards (*Anas platyrhynchos*) and Blue-winged Teal (*A. discors*) were used to test the hypothesis that prairie-nesting ducks exhibit wetland preferences (i.e., select habitat). Mallard pairs did not select wetlands. Mallard broods selected large wetlands with interspersed vegetation when brood density was low. Pairs of Blue-winged Teal selected wetlands, but were inconsistent in their choices. Broods of Blue-winged Teal consistently selected open wetlands with vegetation of low stature, but patterns of wetland selection by broods of Blue-winged Teal bore no consistent relationship to brood density.

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DEPT. BIOLOGY, UNIV. SASKATCHEWAN, SASKATOON, SASKATCHEWAN S7N 0W0, CANADA (JHM AND BRN) AND CANADIAN WILDLIFE SERVICE, PRAIRIE MIGRATORY BIRD RESEARCH CENTRE, SASKATOON, SASKATCHEWAN S7N 0X4, CANADA (TDN). (PRESENT ADDRESS OF JHM: SASKATCHEWAN PARKS AND RENEWABLE RESOURCES, BOX 3003, PRINCE ALBERT, SASKATCHEWAN S6V 6G1, CANADA; PRESENT ADDRESS OF TDN: DEPT. ZOOLOGY, UNIV. GUELPH, GUELPH, ONTARIO N1G 2W1, CANADA.) ACCEPTED 21 JUNE 1985.