# Behaviour Patterns of Mallard *Anas Platyrhynchos* Pairs and Broods in Minnesota and North Dakota

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*Few studies have quantitatively examined* Mallard *behaviour in* North America *during the breeding season. We estimated diurnal time budgets of unmarked* Mallard *males, females, and broods from over* 1,200 *hours of observations at two study areas in western* Minnesota *and south-central* North Dakota *during* 1988-91. *Paired males spent less time feeding and more time alert than did females. Both pair members were engaged in the same behaviour about* 67% *of the time; the male was always most likely to be doing the same thing as the female, but when the male was resting on water or alert, the female was most likely to be feeding. Females with broods spent less time feeding and more time alert and in locomotion than did females without broods. Behaviour of brood females did not differ with brood age or size. Females temporarily left their broods alone* 45 *times—about once for each* 11 *hours of observation. Female absences ranged from* 2 *to* >80 *minutes* ($\bar{x}$>27 *min*); *length of absence was not related to brood age or size. Broods of all ages (a few days old to near fledging) and sizes* (1-10 *ducklings) were left alone on land and water; broods mostly rested and fed during female absences. Brood females spent less time feeding and more time alert than did broods. Females and their broods were engaged in the same behaviour* 62-67% *of the time; the female was always most likely to be doing the same behaviour as her brood, but when the female was resting on water, the brood was most likely to be feeding, and when the female was alert, the brood was most likely to be feeding* (North *Dakota site) or resting on land* (Minnesota *site). Daily activity patterns varied between sites for both pairs and broods. Feeding and resting behaviour showed opposite daily patterns, suggesting that time allocated to feeding constrained time spent resting. Differences between sites and years in time spent feeding by pairs and broods probably reflected varying water conditions and food availability. In light of these differences, we caution researchers against extrapolating from time budget data that are temporally or geographically limited.*

**Keywords: Mallard Behaviour, Pair, Brood, Feeding, Drought, Time Budget, North Dakota.**

Mallards *Anas platyrhynchos* are the most ubiquitous of dabbling ducks, breeding in a wide variety of habitats around the world. Nevertheless, quantitative information about their behaviour patterns is scarce, especially on their primary breeding grounds in North America. Only a few studies document various aspects of behaviour for Mallard pairs (Dwyer *et al.* 1979, Titman 1981) and broods (Ringelman & Flake 1980) in this region.

During a study of Mallard breeding ecology in 1988-91, we documented diurnal behaviour patterns of unmarked pairs and broods on two large study areas in the north-central U.S. Here we present these data in an effort to (1) increase basic information on behaviour patterns of Mallard pairs and broods in this region; (2) provide behavioural comparisons of paired Mallard males and females, of females with and without broods, and of broods of different ages and sizes; and (3) examine variation in behaviour among sites and years.

Behavioural data contribute to our understanding of basic biology and ecology of Mallards, and can help guide decisions related to management of key habitats. Unfortunately, time budget studies are often limited by the small numbers of birds observed and habitats sampled (Afton & Paulus 1992). It is important to know to what extent behavioural observations can be generalised beyond the groups, sites, and conditions from which they were collected. Our data were collected during a period of decreasing water levels at two sites that differed in wetland characteristics. We have attempted to identify patterns that were consistent across groups and conditions and those that were more variable.

## Study areas and methods

During 1988-91, Mallard time-budget data were collected on two 51-km$^2$ circular study areas, one near Detroit Lakes (46°59'N, 96°12'W) in western Minnesota and one near Kulm (46°12'N, 98°53'W) in south-eastern North Dakota. Types of vegetation and wetlands on the study areas were described by Cowardin *et al.* (1998). Wetland basins covered a similar proportion of each study area (Detroit Lakes 17.5%, Kulm 18.7%), but much of the wetland area at Detroit Lakes had a permanent water regime (50.8%), whereas permanent water was negligible at Kulm (1.2%).

Both study areas were in the prairie pothole region, the primary breeding area for North American dabbling ducks (Anderson & Henny 1972). The prairie pothole region is a glaciated landscape characterised by an abundance of small shallow wetlands and by climatic extremes that produce highly variable water conditions (Kantrud *et al.* 1989). By the end of our study, prolonged drought had severely reduced the area of water and the number of breeding pairs on the Kulm study site (Cowardin *et al.* 1998). So few Mallards remained to breed that we did not collect behavioural data at Kulm in 1991.

To find Mallard pairs and broods for observation, we drove throughout the study area by various routes (or walked where roads or trails were unavailable), stopping near wetlands to scan for birds. We observed Mallards through 20-80x spotting scopes and 10x binoculars at distances of roughly 100-450 m. Instantaneous sampling procedures were used to estimate time budgets (Altmann 1974); behaviour of each bird under observation was recorded at 30-second intervals. In most cases, we observed only one pair or one female and brood at a time (93% and 80% of observations, respectively). The behaviour of a brood was recorded as that displayed by the majority of ducklings in view. We attempted to observe focal individuals for 2-hour periods; however, when available focal birds were scarce, observations were sometimes extended to ≤ 4 hours. Many observation periods were <2 hours because focal birds flew or swam out of view ($\bar{x}$= 78 minutes for pairs, 90 minutes for broods). Data were collected several days a week, throughout daylight hours, mainly from late April through June for pairs and from early June to mid-August for broods. In comparisons of females with and without broods, about 97% of data on females without broods came from observations of pairs.

For statistical comparisons between (1) males and females of pairs, (2) females with and without broods, (3) brood females and broods, (4) broods of different ages, and (5) broods of different sizes, we classified behaviours into six categories. These were feeding (obtaining and ingesting food), resting (sitting on water, sitting or standing on land - with or without head tucked or neck contracted), locomotion (swimming, walking, running, flying), comfort (preening, bathing, stretching, scratching, shaking, flapping), alert (extending the neck partially or fully, fixating [staring skyward]), and other (eg, interacting with other birds, vocalising). The proportion of time birds were involved in agonistic interactions (eg, chases, threats) was tabulated, but because the frequency of occurrence of these behaviours was relatively small, they were not analysed as a separate category. To analyse types of feeding behaviour, we separated feeding into categories of immersion: dip (feeding at the water surface, immersing no more than the bill and face), dunk (immersing head or head and neck), tip up (immersing upper body), dive (full body immersion), and other (gleaning off vegetation, pecking off ground, snapping from the air). Because feeding types were not recorded during part of 1988, data from 1988 were not used in analyses of feeding types. Broods were separated into three age groups (1-18, 19-35, and ≥36 days, based on plumage subclasses Ia-Ic, IIa-IIb, and IIc-III of Gollop & Marshall [1954]) and three size groups (1-4, 5-7, and ≥8 ducklings) for analyses of basic behaviours and feeding behaviours. Categories of brood size were chosen to obtain relatively even sample sizes in three groups. Because of limited data on broods at the Kulm site in 1988, those data were dropped from analyses involving broods or females with broods.

The proportion of time spent in each behaviour by each Mallard group (*eg* paired males) was calculated by summing the number of 30-second sampling points assigned to that behaviour and dividing by the total number of sampling points obtained for that group in all observation periods for each site and year (hereafter, site-year). Statistical comparisons between groups (*eg*, males versus females) began with an overall chi-square test for behavioural differences among all combinations of group, site, and year. These chi-square tests used the weighted least squares estimation technique (Grizzle *et al.* 1969) in the Categorical Data Modeling (CATMOD) procedure of SAS (SAS Institute Inc. 1989). Weighting was based on the number of observation periods, which we assumed were independent (*ie*, adequately separated in time and space to prevent over-sampling any individuals). If the overall test was significant ($P \leq 0.05$), we used single degree of freedom, linear contrasts to examine each behaviour category separately for differences between groups by site-year, between groups by site (averaging across years), and between sites by group (averaging across years). We generally chose not to combine sites in analyses because site differences had been documented in some behaviours of these birds in previous analyses (Pietz *et al.* 1993).

To examine the relationship between behaviours of individual pair members, we compared their behaviours using all 30-second sampling intervals for which both birds were in view. We grouped behaviours into the same basic categories listed above (feeding, resting, locomotion, comfort, alert, other), but divided resting into resting on water and resting on land. At a given 30-second sampling point, a pair could exhibit 1 of 49 different combinations of behaviours (*eg* female feeding and male alert). For each study area, the proportion of time spent in each combination was estimated for each year, and yearly proportions were averaged to obtain a single estimate for each behavioural combination. Conditional probabilities were used to evaluate the extent to which the behaviour of one pair member was related to the behaviour of the other. The probability that the male was in behaviour *j*, given that the female was in behaviour *i*, was estimated by counting the number of times the male was in behaviour *j* while the female was in behaviour *i*, and dividing by the total number of times the female was in behaviour *i*. These proportions were compared (for all behaviours except "other") by calculating Bonferroni simultaneous 95% confidence intervals for the differences between each pair of proportions (Scott & Seber 1983). Conditional probabilities were estimated similarly for the female's behaviours relative to those of her mate. Conditional probabilities for behaviours of females and their broods were calculated using the same procedures described for pairs.

The number and length of times females left their broods alone were calculated from observation samples; however, only a minimum length could be calculated if the female was gone when the brood observation began or failed to return before the observation period ended. Separate chi-square goodness-of-fit tests were used to determine if number of absences varied among brood age groups, years, sites, wetland types, or time blocks; expected values were proportional to the number of sampling points. Simple linear correlation tests were used to determine if the length of absences was related to brood age or size.

For males, females, and broods, we graphically explored how the percent time spent in basic behaviours varied with time of day. For each study site, we calculated proportions for each behaviour using eight 2-hour time blocks: <07:00, 07:00-08:59, 09:00-10:59, 11:00-12:59, 13:00-14:59, 15:00-16:59, 17:00-18:59, and ≥19:00 (Central Standard Time). For males and females of pairs, we also calculated the percent of feeding time spent in each type of feeding behaviour for these time blocks at each study site.

## Results

We collected over 1,200 hours of time-budget data (1,096 observation periods) on Mallard pairs and broods during all years and sites combined (**Table 1**). The number of different pairs and broods observed was unknown, but we were able

**Table 1.** Sample sizes of time-budget data collected on Mallard pairs and broods near Detroit Lakes, Minnesota and Kulm, North Dakota during 1988-91.

| | Hours of observations[a] (number of observation periods) | | | | | |
|---|---|---|---|---|---|---|
| | Pairs | | Females | Broods (by age) | | |
| | Males | Females | with broods | 1-18 days | 19-35 days | ≥ 36 days |
| Detroit Lakes | | | | | | |
| 1988 | 131 | 134 (111) | 27 (23) | 4 (7) | 7 (4) | 15 (12) |
| 1989 | 98 | 97 (114) | 90 (84) | 50 (53) | 23 (20) | 17 (12) |
| 1990 | 92 | 88 (83) | 76 (74) | 31 (35) | 27 (21) | 19 (18) |
| 1991 | 61 | 60 (58) | 86 (96) | 29 (39) | 36 (39) | 19 (18) |
| Kulm | | | | | | |
| 1988 | 100 | 97 (89) | | | | |
| 1989 | 89 | 88 (90) | 82 (95) | 51 (62) | 14 (15) | 19 (18) |
| 1990 | 139 | 138 (85) | 138 (94) | 37 (35) | 26 (18) | 76 (41) |
| Total | 710 | 701 (630) | 500 (466) | 203(231) | 133 (117) | 166 (119) |

[a] Excluding time out of sight, and rounded to nearest hour.

to estimate the minimum number of different broods observed using a combination of brood size, age, location, and date to distinguish them. We observed ≥88 broods: 60 from four years in Detroit Lakes and 28 from two years in Kulm. Pairs were observed primarily at semi-permanent (Stewart & Kantrud 1971) wetland basins in both study areas (58% of observation periods); the proportion of observations at seasonal wetland basins was higher in Kulm (26% vs 16%) and the proportion at permanent wetland basins was higher in Detroit Lakes (20% vs 11%). In Detroit Lakes, broods were observed primarily at semi-permanent basins in 1988 (78%) and at permanent basins in 1989-91 (64-94%). In Kulm, broods were observed at semi-permanent basins in 1989 (93%) and at permanent basins in 1990 (96%). This distribution of observation samples generally reflected availability of wetland types on the two study areas in different years.

## *Pair behaviour*

In the overall test for pairs, we found significant behavioural differences among the combinations of group (male, female), site, and year ($\chi^2_{65}$=89.96, $P$=0.022). Two patterns were consistent across site-years (**Figure 1**): females spent more time feeding than did males, and males spent more time alert than did females. Differences between sexes were relatively small and were not statistically significant within site-years ($P\geq0.11$); however, these differences were significant if data were averaged over sites and years (feeding: $\chi^2_1$=4.74, $P$=0.030; alert: $\chi^2_1$=4.87, $P$=0.027). Pairs averaged less than 1% of their time in agonistic interactions (females 0.43% [SE=0.09]; males 0.76% [SE=0.22]).

Within pairs, males and females displayed the same behaviour 67% of the time at Detroit Lakes and 68% at Kulm.

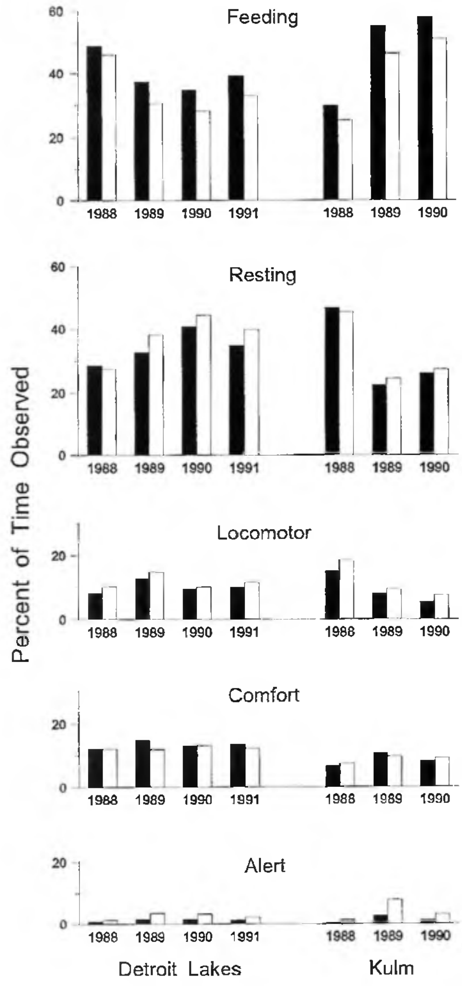

**Figure 1.** Percent of time Mallard females (black bars) and males (open bars) were observed in each of five behaviour categories at two study areas in Detroit Lakes, Minnesota and Kulm, North Dakota, 1988-91. Although females and males differed in how they allocated their time overall, none of the differences between individual bars was statistically sigtnificant ($P>0.05$). Range of time spent in other behaviours (sixth category, not shown) was 0.8-1.4% for females and 1.0-2.6% for males.

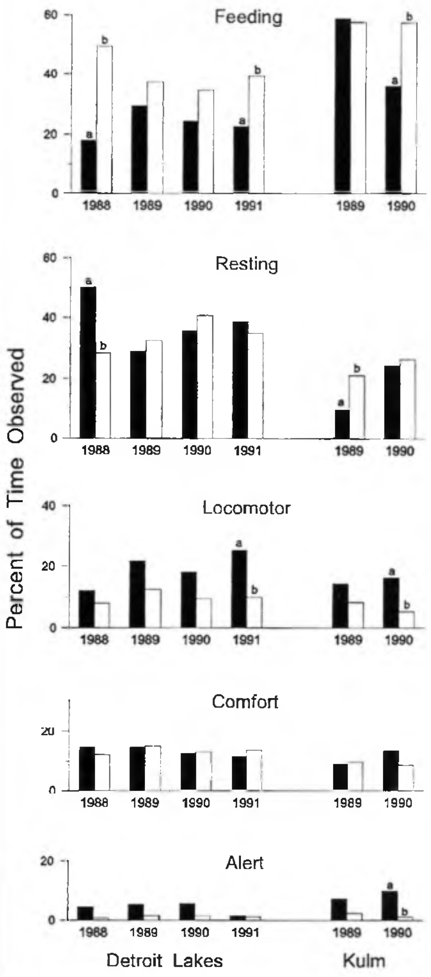

**Figure 2.** Percent of time Mallard females with broods (black bars) and without broods (open bars) were observed in each of five behaviour categories at two study areas in Detroit Lakes, Minnesota, and Kulm, North Dakota, 1988-91. Females without broods are represented largely by observations of females with males. Different letters above bars indicate statistically significant differences ($P\leq0.05$). Range of time spent in other behaviours (sixth category, not shown) was 0.1-3.7% and 0.8-1.3% for females with and without broods, respectively.

**Table 2.** Conditional probabilities[a] of the male's behaviour for each behaviour of the female in Detroit Lakes, Minnesota (1988-91), and Kulm, North Dakota (1988-90). Within rows, proportions that are significantly different ($P \leq 0.05$) are denoted by different letters. Highest probability in each row is shown in bold italics.

| | Male Behaviour | | | | | |
|---|---|---|---|---|---|---|
| | Feed | Rest on water | Rest on land | Locomote | Comfort | Alert |
| Female Behaviour | | | | | | |
| Detroit Lakes: | | | | | | |
| Feed | ***0.688*** *a* | 0.158 *b* | 0.029 *c* | 0.046 *c* | 0.053 *c* | 0.023 *c* |
| Rest on water | 0.319 *a* | ***0.419*** *a* | 0.027 *c* | 0.075 *bc* | 0.115 *b* | 0.028 *c* |
| Rest on land | 0.068 *bc* | 0.024 *cd* | ***0.759*** *a* | 0.032 *cd* | 0.094 *b* | 0.015 *d* |
| Locomote | 0.125 *b* | 0.029 *cd* | 0.017 *cd* | ***0.759*** *a* | 0.052 *c* | 0.005 *d* |
| Comfort | 0.152 *b* | 0.061 *c* | 0.229 *b* | 0.065 *c* | ***0.463*** *a* | 0.021 *c* |
| Alert | 0.133 *b* | 0.061 *cd* | 0.120 *bc* | 0.056 *d* | 0.123 *bc* | ***0.498*** *a* |
| Kulm: | | | | | | |
| Feed | ***0.718*** *a* | 0.104 *b* | 0.025 *c* | 0.060 *bc* | 0.045 *bc* | 0.044 *bc* |
| Rest on water | 0.242 *b* | ***0.536*** *a* | 0.014 *d* | 0.096 *c* | 0.081 *c* | 0.019 *d* |
| Rest on land | 0.071 *b* | 0.033 *bc* | ***0.749*** *a* | 0.048 *bc* | 0.073 *b* | 0.018 *c* |
| Locomote | 0.197 *b* | 0.058 *c* | 0.035 *c* | ***0.630*** *a* | 0.051 *c* | 0.013 *c* |
| Comfort | 0.190 *b* | 0.087 *cd* | 0.161 *bc* | 0.069 *d* | ***0.444*** *a* | 0.035 *d* |
| Alert | 0.157 *b* | 0.024 *d* | 0.045 *cd* | 0.073 *bcd* | 0.095 *bc* | ***0.581*** *a* |

[a] Probabilities in each row do not total 1.0 because the value for "other" behaviours is not listed; probabilities for other were all <0.025.

Conditional probabilities indicated that the male's behaviour was most likely to be the same as that of his mate for all behaviour categories at both sites (**Table 2**). The female's behaviour was most likely to match that of her mate for four of six categories; however, if the male was alert or resting on water, the female was most likely to be feeding (**Table 3**).

## *Female and brood behaviour*

In the overall test for females with and without broods, we found significant behavioural differences among the combinations of group (with, without broods), site, and year ($\chi^2_{55}=118.69$, $P<0.0001$). Females with broods spent less time feeding than did females without broods at both Detroit Lakes ($\chi^2_1=18.16$, $P<0.0001$) and Kulm ($\chi^2_1=3.98$, $P=0.046$), although the difference at Kulm was seen in only one of the two years (**Figure 2**). Females with broods spent more time alert (MN: $\chi^2_1=3.79$, $P=0.052$; ND: $\chi^2_1=9.05$, $P=0.003$) and more time in locomotion (MN: $\chi^2_1=9.41$, $P=0.002$; ND: $\chi^2_1=7.00$, $P=0.008$) than females without broods at both sites. These patterns were consistent across all site-years, although only a few of the differences within site-years were statistically significant (**Figure 2**).

We detected no significant behavioural differences among the combinations of group, site, and year in the overall test for

**Table 3.** Conditional probabilities[a] of the female's behaviour for each behaviour of the male in Detroit Lakes, Minnesota (1988-91), and Kulm, North Dakota (1988-90). Within rows, proportions that are significantly different ($P \leq 0.05$) are denoted by different letters. Highest probability in each row is shown in bold italics.

| | Female Behaviour | | | | | |
|---|---|---|---|---|---|---|
| | Feed | Rest on water | Rest on land | Locomote | Comfort | Alert |
| Male Behaviour | | | | | | |
| Detroit Lakes: | | | | | | |
| Feed | ***0.806*** *a* | 0.040 *b* | 0.053 *b* | 0.035 *b* | 0.058 *b* | 0.004 *c* |
| Rest on water | ***0.632*** *a* | 0.181 *b* | 0.065 *cd* | 0.028 *de* | 0.080 *c* | 0.007 *e* |
| Rest on land | 0.046 *c* | 0.005 *d* | ***0.815*** *a* | 0.007 *d* | 0.121 *b* | 0.005 *d* |
| Locomote | 0.161 *b* | 0.028 *cd* | 0.075 *c* | ***0.642*** *a* | 0.074 *c* | 0.006 *d* |
| Comfort | 0.180 *b* | 0.042 *c* | 0.211 *b* | 0.042 *c* | ***0.508*** *a* | 0.012 *c* |
| Alert | ***0.398*** *a* | 0.052 *d* | 0.170 *bc* | 0.020 *d* | 0.116 *c* | 0.243 *b* |
| Kulm: | | | | | | |
| Feed | ***0.828*** *a* | 0.041 *b* | 0.039 *b* | 0.045 *b* | 0.039 *b* | 0.005 *b* |
| Rest on water | ***0.455*** *a* | 0.348 *a* | 0.069 *b* | 0.051 *b* | 0.067 *b* | 0.003 *c* |
| Rest on land | 0.059 *b* | 0.005 *c* | ***0.845*** *a* | 0.017 *bc* | 0.068 *b* | 0.003 *c* |
| Locomote | 0.249 *b* | 0.060 *c* | 0.094 *c* | ***0.522*** *a* | 0.051 *cd* | 0.009 *d* |
| Comfort | 0.245 *b* | 0.065 *c* | 0.188 *b* | 0.055 *c* | ***0.425*** *a* | 0.015 *c* |
| Alert | ***0.539*** *a* | 0.034 *d* | 0.103 *c* | 0.032 *d* | 0.076 *cd* | 0.209 *b* |

[a] Probabilities in each row do not total 1.0 because the value for "other" behaviours is not listed; probabilities for other were all <0.025.

females with broods of different ages ($\chi^2_{70}$=62.34, $P$=0.73) or in the overall test for females with broods of different sizes ($\chi^2_{70}$=64.37, $P$=0.67). In addition, no patterns were apparent across site-years for females with broods of different ages or sizes.

In the overall test for broods and brood females, we found significant behavioural differences among the combinations of group, site, and year ($\chi^2_{55}$=128.66, $P$<0.0001). Females spent less time feeding (MN: $\chi^2_1$=14.85, $P$=0.0001; ND: $\chi^2_1$=9.22, $P$=0.002) and more time alert (MN: $\chi^2_1$=7.29, $P$=0.007; ND: $\chi^2_1$=15.27, $P$=0.0001) than broods at both sites. Females spent more time resting than broods at Detroit Lakes ($\chi^2_1$=3.83, $P$=0.050), but not at Kulm ($\chi^2_1$=0.01, $P$=0.91). Females with broods averaged less than 0.11% (SE=0.04) of their time in agonistic interactions; broods averaged less than 0.05% (SE=0.03).

Individual females and their broods displayed the same behaviour 62% of the time at Detroit Lakes and 67% of the time at Kulm. Conditional probabilities indicate that the female's behaviour was most likely to be the same as that of her brood for all behaviour categories at both sites (**Table 4**). The brood's behaviour was most likely to match that of the female for four of six categories; however, if the female was resting on water, the brood was most likely to be feeding and, if the female was alert, the brood was most likely to be resting on

**Table 4.** Conditional probabilities[a] of the brood female's behaviour for each behaviour of the brood in Detroit Lakes, Minnesota (1988-91), and Kulm, North Dakota (1989-90). Within rows, proportions that are significantly different ($P \leq 0.05$) are denoted by different letters. Highest probability in each row is shown in bold italics.

| | Female Behaviour | | | | | |
|---|---|---|---|---|---|---|
| | Feed | Rest on water | Rest on land | Locomote | Comfort | Alert |
| Brood Behaviour | | | | | | |
| Detroit Lakes: | | | | | | |
| Feed | ***0.515*** *a* | 0.272 *b* | 0.013 *d* | 0.113 *c* | 0.058 *cd* | 0.027 *d* |
| Rest on water | 0.103 *b* | ***0.636*** *a* | 0.078 *bc* | 0.045 *bc* | 0.098 *b* | 0.026 *c* |
| Rest on land | 0.006 *d* | 0.006 *d* | ***0.747*** *a* | 0.009 *d* | 0.157 *b* | 0.072 *c* |
| Locomote | 0.110 *b* | 0.078 *b* | 0.010 *cd* | ***0.737*** *a* | 0.052 *bc* | 0.009 *d* |
| Comfort | 0.042 *c* | 0.060 *c* | 0.241 *b* | 0.040 *c* | ***0.545*** *a* | 0.068 *c* |
| Alert | 0.030 *b* | 0.052 *b* | 0.039 *c* | 0.033 *b* | 0.011 *b* | ***0.824*** *a* |
| Kulm: | | | | | | |
| Feed | ***0.709*** *a* | 0.051 *bc* | 0.012 *c* | 0.109 *b* | 0.049 *bc* | 0.068 *bc* |
| Rest on water | 0.147 *b* | ***0.339 a*** | 0.197 *ab* | 0.044 *c* | 0.133 *b* | 0.130 *bc* |
| Rest on land | 0.043 *cd* | 0.016 *d* | ***0.624*** *a* | 0.018 *d* | 0.192 *b* | 0.105 *bc* |
| Locomote | 0.156 *b* | 0.026 *c* | 0.010 *c* | ***0.694*** *a* | 0.042 *c* | 0.067 *bc* |
| Comfort | 0.109 *bc* | 0.021 *d* | 0.204 *b* | 0.043 *cd* | ***0.528*** *a* | 0.092 *bc* |
| Alert | 0.008 *b* | 0.023 *b* | 0.017 *b* | 0.033 *b* | 0.023 *b* | ***0.896*** *a* |

[a] Probabilities in each row do not total 1.0 because the value for "other" behaviours is not listed; probabilities for other were all <0.025.

land (Detroit Lakes) or feeding (Kulm) (**Table 5**). A few brood behaviours with the highest probability of occurrence were not statistically different from those having the second highest probability of occurrence (**Table 5**). At Kulm, for example, where feeding time of broods was especially high, broods were likely to be feeding when the females were engaged in any behaviour other than resting on land.

In the overall test for broods in three age groups, we detected no significant differences in basic behaviours among the combinations of group, site, and year ($\chi^2_{70}=61.34$, $P=0.76$). However, some patterns were evident across site-years: broods in the youngest age group consistently appeared to spend less time resting and in comfort behaviours than did older groups (**Figure 3**). Broods of all ages spent very little time alert, averaging 0.32% (SE=0.08) across sites-years.

In the overall test for feeding behaviours of broods in three age groups, we found significant differences among the combinations of group, site, and year ($\chi^2_{56}=161.31$, $P<0.0001$). Surface feeding (dip) decreased and tip-up feeding increased with age (**Figure 4**). Averaged across years, dunk feeding increased with age at Kulm (1vs2: $\chi^2_1=37.95$, $P<0.0001$; 1vs3: $\chi^2_1=87.71$, $P<0.0001$) but not at Detroit Lakes (1vs2: $\chi^2_1=1.52$, $P=0.22$;

**Table 5.** Conditional probabilities[a] of the brood's behaviour for each behaviour of the brood female in Detroit Lakes, Minnesota (1988-91), and Kulm, North Dakota (1989-90). Within rows, proportions that are significantly different ($P \leq 0.05$) are denoted by different letters. Highest probability in each row is shown in bold italics.

| | Brood Behaviour | | | | | |
|---|---|---|---|---|---|---|
| | Feed | Rest on water | Rest on land | Locomote | Comfort | Alert |
| Female Behaviour | | | | | | |
| Detroit Lakes: | | | | | | |
| Feed | ***0.853*** *a* | 0.021 *c* | 0.006 *c* | 0.087 *b* | 0.016 *c* | 0.000 *c* |
| Rest on water | ***0.660*** *a* | 0.193 *b* | 0.009 *de* | 0.091 *c* | 0.033 *cd* | 0.001 *e* |
| Rest on land | 0.026 *c* | 0.020 *c* | ***0.834*** *a* | 0.010 *c* | 0.110 *b* | 0.001 *c* |
| Locomote | 0.229 *b* | 0.011 *c* | 0.010 *c* | ***0.716*** *a* | 0.018 *c* | 0.000 *c* |
| Comfort | 0.189 *b* | 0.040 *c* | 0.283 *ab* | 0.081 *c* | ***0.401*** *a* | 0.000 *d* |
| Alert | 0.286 *a* | 0.034 *c* | ***0.415*** *a* | 0.043 *c* | 0.160 *b* | 0.055 *c* |
| Kulm: | | | | | | |
| Feed | ***0.925*** *a* | 0.005 *b* | 0.011 *b* | 0.037 *b* | 0.019 *b* | 0.000 *b* |
| Rest on water | ***0.713*** *a* | 0.135 *b* | 0.043 *cd* | 0.064 *bc* | 0.040 *cd* | 0.002 *d* |
| Rest on land | 0.069 *bc* | 0.033 *cd* | ***0.714*** *a* | 0.010 *cd* | 0.163 *b* | 0.001 *d* |
| Locomote | 0.443 *a* | 0.005 *b* | 0.014 *b* | ***0.506*** *a* | 0.024 *b* | 0.001 *b* |
| Comfort | 0.287 *ab* | 0.022 *c* | 0.219 *b* | 0.044 *c* | ***0.421 a*** | 0.001 *c* |
| Alert | ***0.555*** *a* | 0.030 *c* | 0.166 *b* | 0.099 *bc* | 0.102 *bc* | 0.044 *c* |

[a] Probabilities in each row do not total 1.0 because the value for "other" behaviours is not listed; probabilities for other were all <0.025.

1vs3: $\chi^2_1=2.93$, $P=0.09$). Broods of all age groups made feeding dives, but this behaviour was too rare to test for age-group differences.

In the overall test for broods in three size groups, we found no significant behavioural differences among the combinations of group, site, and year ($\chi^2_{70}=62.41$, $P=0.73$) and no patterns evident for any specific behaviours across site-years. In the overall test for feeding behaviours of broods in three size groups, we found significant differences among the combinations of group, site, and year ($\chi^2_{56}=90.17$, $P=0.0026$); however, there were no patterns evident for any feeding type across site-years.

## *Female absences from broods*

Females temporarily left at least 32 different broods alone 45 times in the 506 hours that broods were in sight—ie about once in every 11 hours of observation. These female absences averaged > 27 minutes and ranged from 2 to > 80 minutes (only a minimum length was known for 11 absences). The numbers of absences recorded did not differ from expected for each site, year, and wetland type (*P*-values for all chi-square tests >0.25). Absences occurred in temperatures ranging from 13° to 38°C and wind speeds from 0 to 7.9 m/sec. Rain occurred during at least two absences. Females were observed leaving broods as early as 05:14, as late as 19:37, and in all hours except 12:00-13:00. There were fewer absences than expected in the 4 hours around noon than in earlier or later periods of the day ($\chi^2_2$=5.95, $P$=0.051).

The brood was in view at the time the female departed on 38 of the 45 occasions. Females primarily left broods on shore at Kulm (15 of 17) and on water at Detroit Lakes (13 of 21). In 10 cases, broods moved from shore to water (6) or from water to shore (4) while the female was absent. When females left, broods were most often resting (63%), feeding (18%), or swimming (11%). Most broods changed behaviours while the female was absent, and about half the broods fed during the 45 absences.

Broods from a few days old to near fledging were left alone temporarily. At Detroit Lakes, female absences were proportional to the amount of behavioural data collected for each age class of ducklings. At Kulm, absences were not proportionally distributed by brood age ($\chi^2_2$=8.24, $P$=0.016); there were proportionally fewer absences from the youngest broods and more absences from the oldest broods. Broods ranging in size from 1 to 10 ducklings were left alone; absences were evenly distributed among broods of different size classes at both sites. The length of absence was not correlated with brood age (using 7 plumage/age classes, $r$=0.002, $P$>0.99) or brood size (using number of ducklings, $r$=0.314, $P$=0.07). Of the 32 broods temporarily left alone, eight were left twice (age classes Ia-III); one brood of 10 ducklings (class III) was left 6 times in 16 days. Three broods (Ia-III) were left twice during the same observation period. No duckling deaths were observed during any of the female absences.

## *Site and year differences in behaviour*

In 1988, pairs differed significantly between sites in percent time spent feeding (female: $\chi^2_1$=7.94, $P$=0.005; male: $\chi^2_1$=10.00, $P$=0.002) and resting (female: $\chi^2_1$=7.07, $P$=0.008; male: $\chi^2_1$=7.09, $P$=0.008). In subsequent years, pairs also differed significantly between sites in time spent feeding (female: $\chi^2_1$=15.90, $P$=0.0001; male: $\chi^2_1$=14.18, $P$=0.0002) and resting (female: $\chi^2_1$=6.85, $P$=0.009; male: $\chi^2_1$=10.38, $P$=0.001) but in the opposite direction (**Figure 1**). Mallard pairs spent more time feeding at Detroit Lakes than at Kulm during 1988, and more time feeding at Kulm than at Detroit Lakes in subsequent years. Resting behaviour showed patterns opposite to those of feeding behaviour.

During 1988 at Detroit Lakes, females with broods showed the opposite pattern seen in pairs: they spent less time feeding and more time resting than in subsequent years (**Figure 2**). After 1988, site differences exhibited by females with broods were the same as those seen in pairs: they spent more time feeding and less time resting at Kulm than at Detroit Lakes. Across years, females with broods showed significant site differences in feeding ($\chi^2_1$=27.18, $P$<0.0001) and resting ($\chi^2_1$=24.36, $P$<0.0001) behaviour. Broods spent less time feeding ($\chi^2_1$=20.32, $P$<0.0001) and more time resting ($\chi^2_1$=8.99, $P$=0.003) and in locomotion ($\chi^2_1$=5.69, $P$=0.017) at Detroit Lakes than at Kulm (**Figure 3**). Broods in the two older age groups spent more time dip feeding (grp 2: $\chi^2_1$=14.40, $P$=0.0001; grp 3: $\chi^2_1$=19.61, $P$<0.0001) and less time dunk feeding (grp 2: $\chi^2_1$=6.82, $P$=0.009; grp 3: $\chi^2_1$=8.70, $P$=0.0032) at Detroit Lakes than at Kulm (**Figure 4**).

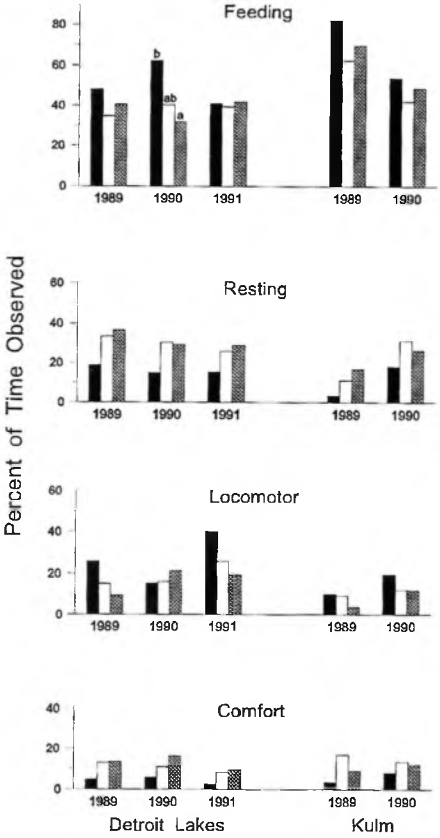

**Figure 3.** Percent of time Mallard broods of different ages were observed in each of four behaviour categories at two study areas in Detroit Lakes, Minnesota, and Kulm, North Dakota, 1988-91. Brood age groups were 1-18 days (black bars), 19-35 days (open bars), and ≥36 days (gray bars), based on plumage subclasses Ia-Ic, IIa-IIb and IIc-III of Gollop & Marshall (1954). Different letters above bars indicate statistically significant differences ($P \leq 0.05$). Range of time spent alert was 0.0-1.0% and in other behaviours was 0.1-3.5%.

### *Daily activity patterns*

Males and females showed similar patterns of behaviour across most hours of the day (**Figure 5**). Site differences were apparent in feeding and resting patterns of both sexes. At Detroit Lakes, feeding levels were highest in mid-morning and at the end of the day; feeding levels were lowest in early morning and around noon. At Kulm, feeding levels were highest around noon and at the end of the day. Patterns of resting behaviour were opposite those of feeding.

Types of feeding behaviour also showed patterns that were similar between sexes and different between sites. At Detroit Lakes, tip-up feeding peaked around noon and dunk feeding peaked in late afternoon. At Kulm, dunk feeding peaked around noon and tip-up feeding peaked at the end of the day. Surface feeding peaked at the end of the day at Detroit Lakes and in early morning and at 17:00-19:00 at Kulm .

Females and broods showed low feeding levels during late morning and high feeding levels near the end of the day (**Figure 6**) at both sites. Females at Detroit Lakes exhibited relatively low feeding levels throughout the day compared to the other groups. Patterns of resting behaviour were opposite those of feeding patterns for both females and broods.

## Discussion

### *Pair behaviour*

Mallard females spent a higher proportion of time feeding than males presumably to meet the nutritional demands of producing and incubating eggs. This difference between sexes in time observed feeding has been reported for small samples of

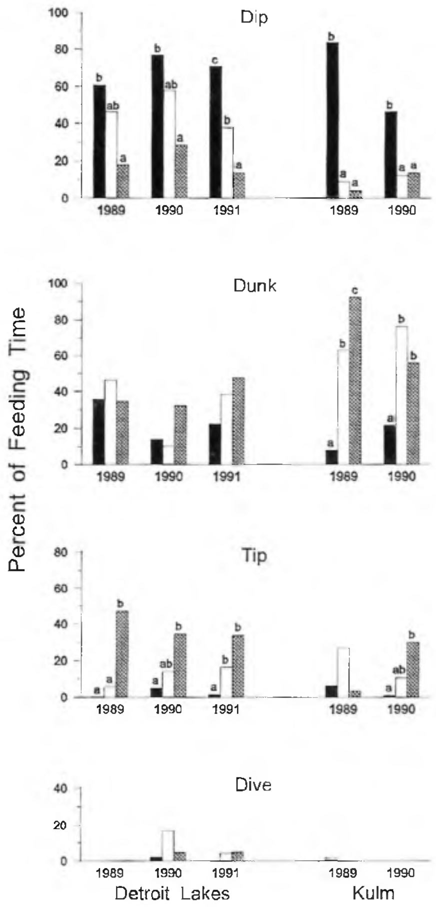

**Figure 4.** Percent of feeding time Mallard broods of different ages were observed using each of four feeding methods at two study areas in Detroit Lakes, Minnesota, and Kulm, North Dakota, 1989-91. Feeding methods include dip (immersing no more than the bill and face), dunk (immersing head or head and neck), tip up (immersing upper body), and dive (full body immersion). Brood age groups were 1-18 days (black bars), 19-35 days (open bars), and ≥36 days (gray bars), based on plumage subclasses Ia-Ic, IIa-IIb, and IIc-III of Gollop & Marshall (1954). Different letters above bars indicate statistically significant differences ($P \leq 0.05$).

marked Mallards in the prairie pothole region of North America (Titman 1973, 1981; Dwyer *et al.* 1979) and in northern Sweden (Asplund 1981). Note that, in these studies and ours, incubating females could only be observed while they were away from their nests; thus the observed amount of feeding time for females may be biased high relative to males if a significant proportion of pair observations involve incubating females. However, given the short time that incubating females are off the nest (Gloutney [1989] estimated a mean of 148 min/day), most of our pair data likely involved females laying eggs or preparing to nest or renest.

Overall, males in our study spent more time alert than females, which one would expect if males were attempting to guard their mates. That males guarded their mates, at least in part, to provide them with undisturbed feeding time was suggested by the fact that, within pairs, the female was most likely to be feeding while the male was alert or resting on water. Although mate guarding undoubtedly serves other functions (eg protection of genetic paternity [Goodburn 1984]), its importance in providing undisturbed feeding time for females has been noted in Mallards (Titman 1983; Mjelstad & Sætersdal 1988) and other waterfowl (McKinney 1988; Paquette & Ankney 1998).

## Female brood care

That Mallard females with broods spent more time alert than females without broods is not surprising; an increase in alert behaviour among adults with broods has been documented in other species of waterfowl as well (Afton & Paulus 1992). In our study, females with broods also spent more time in locomotion, which may

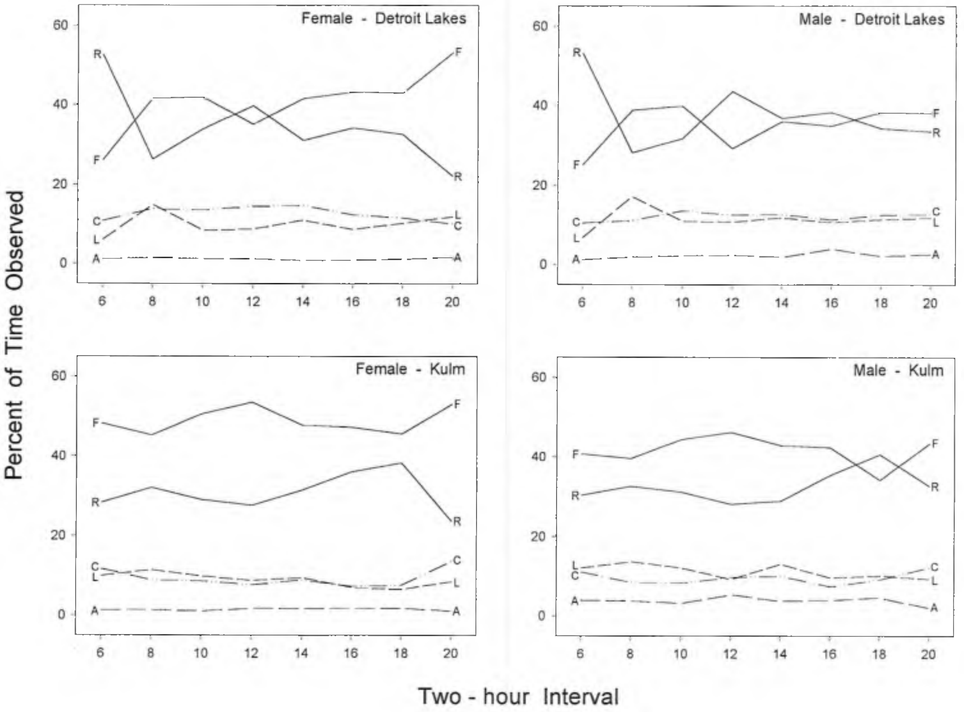

**Figure 5.** Percent of time Mallard females and males were observed in feeding (F, ——), resting (R, ——), locomotor (L, - - - - ), comfort (C, — · · — ), and alert (A, — — — ) behaviours at two study areas in Detroit Lakes, Minnesota, and Kulm, North Dakota, 1988-91, throughout the daylight hours. Percentages are plotted at the mid-point of each two-hour interval; hours are in Central Standard Time.

reflect time spent monitoring active ducklings and leading broods to feeding and resting sites. Females with broods generally spent less time feeding than females without broods, but it is unclear whether this reflects demands of brood care or the fact that females without broods are largely represented by paired females observed earlier in the season. In Sweden, Asplund (1981) too noted a lower proportion of feeding time for female Mallards during the brood period than during egg-laying and incubation.

Further evidence of vigilance by brood females was suggested by the fact that they spent more time alert and less time feeding than their broods. That the brood was most likely to be feeding while the female was alert (Kulm) or resting on water (both sites) specifically reflects female monitoring of ducklings while they were feeding on water.

Time allocations of females with newly hatched broods may be a compromise between the needs of ducklings for parental care and the need for females to regain body mass lost during incubation (Afton & Paulus 1992). As ducklings grow older, their vulnerability and the female's nutritional needs should both decline, so one might expect females to spend more time alert and feeding when their broods are younger. Hickey & Titman (1983) found that female Black Ducks (*Anas rubripes*) with class I broods fed more than those with class II broods, but found no difference in the amount of time females spent alert. Rushforth Guinn & Batt (1985) found no difference in time spent feeding by female Northern Pintails (*Anas acuta*) with class I and II broods, and recorded more time alert for females with class II broods. For female Mottled Ducks, Paulus (1984) found that time spent feeding declined but time spent alert did not change as broods matured. For Mallards, we found no evidence of any behavioural differences among females with broods of different ages.

According to a model developed by Lazarus & Inglis (1986), parental investment is expected to remain constant for different brood sizes if the investment benefits all young simultaneously (eg alert behaviour) and if predators generally don't take the entire brood when they strike. They suggest that such conditions are more likely to occur in waterfowl and other birds with precocial young. The fact that we found no differences in female behaviour related to brood size supports the prediction of this model. Similarly, the amount of time devoted to brood care was not related to brood size in studies of Northern Pintails (Rushforth Guinn & Batt 1985) or Mottled Ducks (Paulus 1984).

Female absences from broods have been observed in many duck studies, but there is no consensus on why females occasionally leave broods alone. Afton & Paulus (1992) noted that females may take these breaks to spend time at sites more suitable to their own needs (eg "to feed, loaf, or engage in social activities..."), to avoid competing with their offspring for food, or to scout for more favourable locations for their broods. If females are scouting for wetlands with more invertebrates, their scouting trips may be timed, in part, to periods when aquatic invertebrates with diel vertical movements are close to the surface. This may explain the lull in female absences during midday.

Duckling deaths rarely have been documented during female absences; however, Talent *et al.* (1983) recorded the loss of two entire broods that were left alone during inclement weather. The lack of duckling deaths during female absences in other studies may reflect the rarity of

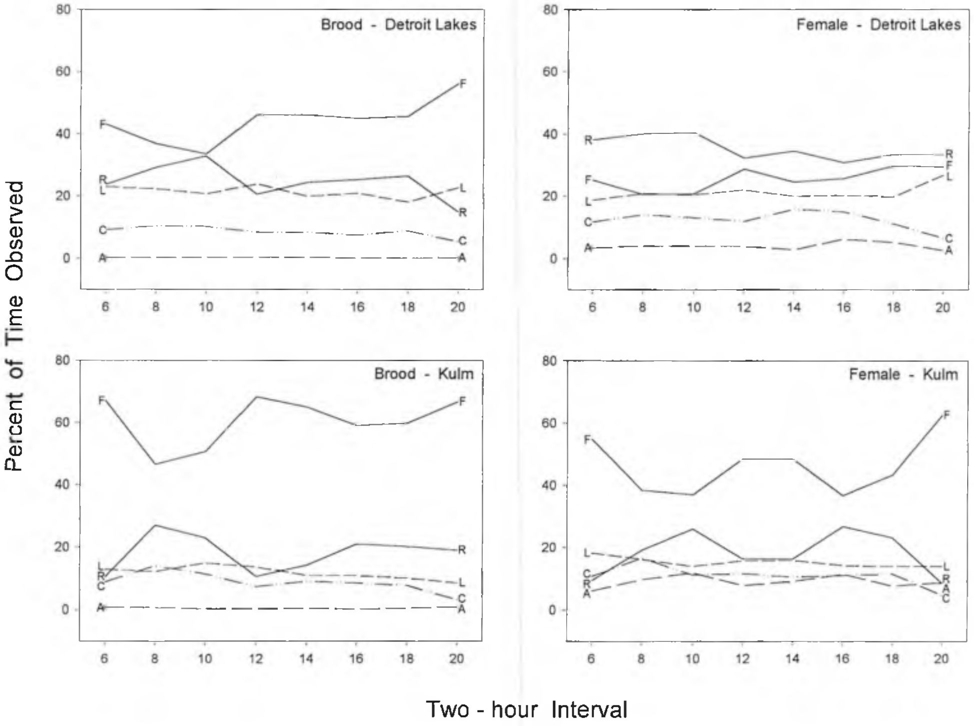

**Figure 6.** Percent of time Mallard broods and females were observed in feeding (F, ), resting (R, ), locomotor (L, - - - - ), comfort (C, — · · — ), and alert (A, — — —) behaviours at two study areas in Detroit Lakes, Minnesota, and Kulm, North Dakota, 1988-91, throughout the daylight hours. Percentages are plotted at the midpoint of each two-hour interval; hours are in Central Standard Time.

observing duckling losses at all. We observed only one Mallard duckling loss during more than 500 hours of brood observations (a duckling depredated by a Black-crowned Night-Heron [*Nycticorax nycticorax*] despite an attempted defence by the brood female). Risks to ducklings from predation and exposure probably are lower during daylight (when observations occurred) than at night.

## *Brood behaviour*

Although broods in our study showed no significant differences in basic time budgets among age groups, we noted a tendency for older broods to spend more time in maintenance behaviours (resting, comfort) than broods in the youngest group. Likewise, Ringelman & Flake (1980) found that Mallard broods in their South Dakota study area spent similar amounts of time feeding but more time in maintenance behaviours (loafing, sleeping) as they got older. Increased time in comfort behaviours among older ducklings may reflect increased preening activity as their juvenile feathers developed. Hickey & Titman (1983) noted a higher level of comfort behaviour in class III broods of Black Ducks, coinciding with their acquisition of new plumage.

Changes in feeding methods with brood age appear to reflect differences in duckling capabilities as they develop. As in our study, Ringelman & Flake (1980) noted that class I Mallard ducklings fed primarily at the surface; the proportion of subsurface feeding (immersing at least the head) became more common by age-class II. Chura (1961) stated that class I ducklings tend not to submerge their bill above the nares. In our study, however, class I ducklings fed with at least their heads submerged up to 36% of the time. Other studies have indicated that tip-up feeding was first seen in class II ducklings (Beard 1964, Pehrsson 1979, Ringelman & Flake 1980) and reached highest levels in the oldest age group. Although our findings were similar, we documented some tip-up behaviour in class I ducklings in all site-years (range 0.2-6.2% of feeding time). Likewise, although dive feeding was relatively rare, it was not restricted to any age group. The flexibility we observed in feeding methods at different ages suggests that morphological and physiological limitations may play a smaller role in development of foraging techniques of Mallards than previously believed. In a study of duckling/fish competition for food (Cox *et al.* 1998), Mallard ducklings less than two weeks old were observed diving and capturing fish in three of five experimental ponds that were stocked with fathead minnows (*Pimephales promelas*) (J. E. Austin & P. J. Pietz, unpubl. data). Feeding methods of broods likely reflect, in part, types of foods available and the frequency with which ducklings encounter them.

## *Daily activity patterns*

For Mallard pairs and broods, patterns of feeding and resting behaviour appeared to be mirror images of each other across hours of the day (**Figures 5** and **6**); this suggests that the amount of time spent feeding constrained the amount of time spent resting. If there are consequences of this constraint, they most likely would have occurred when feeding levels were highest—eg 82% for young broods at Kulm in 1989. Ducklings that spent such a large proportion of their time feeding may have been more susceptible to exposure and predation.

It is commonly believed that dabbling

ducks have peaks in feeding activity at the beginning and end of the day (Chura 1963, Winner 1972, Titman 1981, Figala *et al.* 1990), probably to recover from and prepare for a period of night-time fasting. Some support for these patterns has been shown for Mallard broods (Chura 1963, Ringelman & Flake 1980). Birds in our study showed some of these peaks, but feeding activity was lowest in early morning for pairs at Detroit Lakes. Water conditions on this study area (as discussed in the next section) may have provided more opportunities for nocturnal foraging; if so, this would have reduced the need for a morning recovery period. During the breeding season, daily feeding patterns probably reflect, in part, changes in availability of aquatic invertebrates. Evening peaks in feeding can occur where aquatic insects emerge near dusk; morning feeding peaks can occur where low oxygen levels push Cladocera closer to the water surface (Swanson 1977). At higher latitudes, peaks in feeding activity of dabbling ducks have been linked to chironomid emergence near noon (Sjöberg & Danell 1982).

Feeding methods also may show daily patterns, especially where aquatic invertebrates move vertically through the water column. Pöysä (1989) found that Green-winged Teal (*Anas crecca*) fed deeper as the morning progressed, increasing their proportions of feeding with head, neck, and upper body submerged. He attributed their changes in feeding method to decreasing availability of prey near the water surface, resulting from prey depletion or disturbance by foraging birds. Presumably, similar shifts in feeding depth should occur with diurnal movements of invertebrates linked to environmental variables such as light and oxygen. If prey such as Cladocera and chironomids are lower in the water column at midday, it is not surprising that we observed highest levels of tip-up feeding around noon for Mallard pairs at Detroit Lakes. It is not clear, however, why tip-up feeding of pairs reached highest levels at the end of the day at Kulm.

## Site and year differences

Many factors could have contributed to site and year differences that we observed in Mallard behaviours (eg vegetation effects on visibility, age ratios and reproductive effort of females, predator types and densities). We will confine our discussion to potential factors for which we have some evidence.

The Detroit Lakes site had larger and deeper wetlands than were available on the Kulm site; this probably affected the types of aquatic invertebrates present. Aquatic invertebrates also are likely to have greater vertical movement in deeper wetlands, affecting their accessibility to dabbling ducks both daily and seasonally (Swanson & Sargeant 1972, Swanson 1977, King & Wrubleski 1998). It is possible that these factors led to more nocturnal feeding at the Detroit Lakes site. If so, the lower proportion of time spent feeding by most groups in most years at this site may simply represent less feeding during the day rather than lower total feeding time. However, this would not explain why the opposite pattern was seen among pairs in 1988: observed time spent feeding was relatively high in Detroit Lakes and low in Kulm in that year.

Patterns we saw in all years and sites could reflect increased feeding time by birds where drought reduced the abundance of aquatic invertebrates. Although pond area generally declined on both of our study areas (Cowardin *et al.*

1998), the drop was about 90% at Kulm and only 40% at Detroit Lakes from 1987 to 1991. Because Kulm had more than twice as many ponds when the drought began, and was especially rich in the type of shallow ponds that produce high densities of aquatic invertebrates (Euliss *et al.* 1999), food may still have been relatively plentiful at the Kulm site in 1988, even as water levels began to decline precipitously. In subsequent years, however, water levels did not recover enough to reflood wetland edges that had dried in previous years. As this reflooding is vital for the productivity of aquatic invertebrates in prairie pothole wetlands (Euliss *et al.* 1999), the food supply at the Kulm site probably fell to low levels and remained low for the duration of the study. In Detroit Lakes, 1988 was the driest year of the study (in terms of precipitation), after which seasonal reflooding was probably adequate to improve food availability.

Changing water levels also may have affected types of feeding behaviour used by broods at Kulm. Tip-up feeding reached highest levels among the oldest age group in all site-years except Kulm-1989 (**Figure 4**). During that year, broods were observed almost entirely on semi-permanent wetlands, which were drying up as a result of severe drought. Many wetlands were so shallow that the oldest ducklings could reach the bottom without tipping up. By 1990, nearly all semi-permanent wetlands at Kulm were dry and broods fed primarily on the remaining permanent wetland, where the water was deeper; in 1990, tip-up feeding again was at highest levels in the oldest broods. Similar changes in feeding methods have been documented for adult Mallards in response to changing water levels and food availability (Danell & Sjöberg 1982).

In our study, some behaviour patterns emerged that appeared to be consistent across sites and years, despite differences in wetland types on our two sites and differences among years at each site resulting from drought. These included differences between males and females, between females with and without broods, and between females and their broods in time spent feeding and alert. Relative importance of various feeding methods among broods of different ages also appeared to be fairly consistent across site-years. These examples likely reflect mate guarding, maternal care, and duckling development or experience, respectively. Presumably, these patterns are the most general, and are most likely to be seen in other Mallard populations and other habitats. Even for these behaviours, however, the actual percentages of time spent varied greatly among site-years. Females with broods, for example, varied in feeding time from 18% (Detroit Lakes 1988) to 59% (Kulm 1989). Aspects of behaviour that showed considerable variation across sites and years in our study should serve as caution against generalising from data sets that are geographically or temporally limited.

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