

## Wetland fidelity of female Mallard *Anas platyrhynchos* and Gadwall *Anas strepera* during brood rearing

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Occurrence of and factors affecting fidelity to brood-rearing areas have received little attention in ducks; thus, data from individually marked female Mallard *Anas platyrhynchos* and Gadwall *Anas strepera* collected over 5–7 years were used to investigate these patterns and processes. First, it was determined whether the 30-day tracking period used in most recent brood survival studies was sufficient for characterising wetland use. Radio-marked Mallard ( $n = 15$ ) that were tracked consistently for 50 days had moved 93% of total distance travelled within 30 days whereas Gadwall ( $n = 8$ ) had travelled > 99% of total distance moved in 40 days. Thus, a 30-day tracking period appeared adequate for both species. In several instances, marked ducklings of female parents that had been killed or had abandoned their brood were recaptured fully grown later in summer or when nesting in later years. Using recaptures of web-tagged ducklings from 69 Mallard and 49 Gadwall broods, an estimate was made of how often errors occurred in declaring total brood loss in radio-marked broods. In most years, designation of complete brood loss was about 5% higher than adjusted estimates and, overall, brood loss declined by 9% in Mallard and 13% in Gadwall after accounting for recaptures. In Mallard, 33% of female offspring ( $n = 15$ ) and 50% of female parents ( $n = 12$ ) reused at least one brood-rearing wetland in a later year, as did most female Gadwall offspring (75%,  $n = 4$ ) and all three female Gadwall parents. Female Mallard offspring spent 2–26 days (mean = 11 days) on their natal brood ponds and female parents spent 4–30 days (mean = 15 days) there; ranges were 2–21 days for female Gadwall offspring and 2–7 days for female parents. Logistic regression analysis of wetland reuse revealed that female parents had greater fidelity than female offspring to previously used wetlands. Probability of reusing wetlands was unrelated to previous fledging success. Distances from previously used brood-rearing or natal wetlands to wetlands used  $\geq 1$  year later were much closer together than expected (when compared with distances and directional bearings to randomly selected, brood-rearing wetlands). Thus, females of both species tended to return to specific wetlands or brood-rearing areas they had

used previously. In philopatric duck species, local populations of brood-rearing females could be well structured spatially according to family lineage in areas of stable wetland conditions.

**Key Words:** *Anas platyrhynchos*, *Anas strepera*, brood-rearing, brood loss, movements, Saskatchewan, wetland fidelity

## Introduction

During the past 10 years, much research has focused on evaluating sources of variation in survival of ducklings (Guyn & Clark 1999; Krapu *et al.* 2000; Rotella & Ratti 1992), an aspect of their ecology that had previously been neglected. Despite these important advances, some issues remain unresolved. Although duckling mortality is typically low after 15–20 days and brood movements apparently are most frequent when broods are < 15 days old (Dzus & Clark 1997; Talent *et al.* 1982), it is rarely established whether movements stabilise within 30 days, a critical issue for determining wetland fidelity. Mauser *et al.* (1994b) reported relatively high frequency of movements > 1,000 m by 4-week-old Mallard *Anas platyrhynchos* broods. Furthermore, most studies assume that brood mortality is complete if the attending female dies or abandons its brood (e.g. Rotella & Ratti 1992; Talent *et al.* 1983), despite some evidence to the contrary (Gendron & Clark 2000; Mauser *et al.* 1994a); this assumption ignores the possibility that ducklings could survive well when environmental conditions are favourable or if adopted by other females. The authors address these and other deficiencies using data for individually marked Mallard and Gadwall *A. strepera* collected over periods of 5–7 years.

Nest site fidelity is well-documented in several duck species (Anderson *et al.* 1992) but occurrence of and factors affecting fidelity to brood-rearing locations have received limited attention. Seymour & Jackson (1996, p. 1162) indicated that some brood-rearing female Black Ducks *A. rubripes* returned to natal brood-rearing areas. Because nest site fidelity is strong in Mallard and Gadwall (Clark & Shutler 1999; Lokemoen *et al.* 1990), fidelity to brood-rearing wetlands might also be expected because some evidence for this behaviour has been reported in Canvasback *Aythya valisineria* (Leonard *et al.* 1996), Barrow's Goldeneye *Bucephala islandica* (S. Boyd, Canadian Wildlife Service, personal communication) and Bufflehead *B. albeola* (G. Gauthier, Laval University, personal communication), species that also display strong nesting site fidelity. However, fidelity could be stronger in experienced females than in their naïve female offspring, as reported for nest site fidelity (i.e. natal versus breeding dispersal in birds, Greenwood & Harvey 1982). In addition, females that fledge relatively more ducklings should exhibit greater fidelity than females with low or no fledging success (e.g. Lindberg & Sedinger 1998). Increasing distance between successive nest attempts could weaken fidelity if distance to previously used wetlands exceeds the distance that females are willing or able to move

broods. Finally, it seems plausible that fidelity estimates could be determined more reliably in females that are radio-tracked for longer periods. These hypotheses and methodological issues have not been addressed in ducks (Anderson *et al.* 1992, p. 376) and have apparently attracted only limited attention in waterfowl (reviewed by Lindberg & Sedinger 1998). Therefore, two methodological issues that impinge on reliably determining brood survival and movements were considered, specifically by evaluating the number of days required to determine the full range of movements made by brood-rearing females, and then by gauging the error rate when estimating total brood loss. These factors also influence the study's main objective: determining whether or not female dabbling ducks exhibit wetland fidelity when raising ducklings and, if so, identifying correlates of site fidelity.

## Methods

Work was conducted on St. Denis National Wildlife Area (NWA) and vicinity, located about 50 km east of Saskatoon, Saskatchewan, Canada, from 1994 to 2000. The NWA (385 ha) is characterised by fields of planted herbaceous cover, areas of native grass, shrubs and trees, annually tilled cropland, and approximately 100 wetland basins that comprise about 10% of the NWA area and vary in size (e.g. < 0.5 to 2 ha) and permanency (details below). The area surrounding the NWA is rolling terrain with a high density of relatively small, isolated wetland basins, and land use is dominated by cattle pasture and forage and spring-

seeded crop production. The study was conducted during a period of consecutive wet years in this region of the Canadian prairies, so numerous semi-permanent and permanent wetlands were found within 2–3 km of the NWA. Female Mallard and Gadwall were captured on nests, usually during late incubation, and nasal-tagged for survival studies (e.g. Arnold & Clark 1996; Dufour & Clark 2002), and most ducklings were web-tagged before hatching (e.g. Alliston 1974). Mallard and Gadwall typically nested in dense herbaceous cover, shrubs or wooded habitats located at varying distances from wetlands (see Clark & Shuttler 1999 for further details). During 1994–97, a sample of females was also equipped with external radios for a study of brood survival (Gendron & Clark 2002). This created a unique opportunity to mark adult female parents and their female offspring in subsequent years to determine the extent and correlates of brood-site fidelity. All capture and marking protocols were reviewed and approved by the University of Saskatchewan's Animal Care Committee on behalf of the Canadian Council on Animal Care.

Nesting females were captured until 2000, so female offspring of radio-marked female parents could be detected up to three years after the radio-tracking study had ended. Apparent estimates of total brood loss were adjusted to account for these recaptures, providing insights into the implications of declaring total brood loss during duckling survival studies. Brood survival was defined as the percentage of broods with a least one surviving 30-day-old duckling.

This estimate was adjusted annually to account for ducklings, assumed dead, encountered later in life. This is a *minimum* adjustment, however, because it involved recaptures of surviving individuals that retained web tags (Blums *et al.* 1996) and either remained on the study area as older ducklings or recently fledged birds, or returned in subsequent years to nest on the study area (i.e. detection probability [ $P_d$ ] < 1).

### **Distances moved during brood-rearing**

A female would move her brood from the nest to one or more wetlands shortly after hatching. Beginning with the distance between the nest and the first-used wetland, distances were measured from aerial photographs (approx. 1:10,000) using EASYDIJ digitising software (Geocomp Ltd. 1990) assuming straight-line movement between used wetlands. Direction (degrees from north) of movement was measured using a protractor. Distances between successive nesting attempts (i.e. a female parent's breeding dispersal or a female offspring's natal dispersal) were measured from a detailed map of the NWA using a standard ruler. Because some breeding females were tracked for up to 40 (Gadwall) or 50 (Mallard) days after hatching, summed distance moved up to 30 days post-hatching (when most observations have ended in this and other studies) could be compared with the total distances moved over longer periods.

### **Measuring fidelity to brood-rearing wetlands**

Measures of fidelity were occurrence and number of days that the same wetland(s) was used either by a brood-rearing female parent (from one year to another) or by a female offspring in its first known brood-rearing event. The brood-rearing wetland was defined as being the final wetland used and as having the longest period of use; in all cases, this designation was unambiguous. Most birds were radio-tracked for two years so they appear only once in analyses; only two Mallard tracked as female offspring were subsequently tracked as parents. Fidelity was also determined by comparing use of wetlands in year  $t$  versus use of randomly selected wetlands in year  $t$ . A random distance from a parent's nest was selected from a uniform distribution between 11–4,229 m, this being the observed range of distances moved from nests to wetlands by brood-rearing females (see Gendron & Clark 2002 for additional information), and this distance was matched with a random bearing taken from a uniform distribution between 1° and 360°. Locations were plotted on maps and those on semi-permanent and permanent wetlands were retained as randomly selected wetlands. A uniform distribution was used in each case because semi-permanent and permanent wetlands were abundant during the study, so brood-rearing females encountered these wetlands on or in any direction from the NWA.

Except in 1995, when there were fewer July and August wetlands ( $n = 38$  and 30, respectively), numbers of

flooded wetlands were comparable among years (1994:  $n = 78$  and  $50$ ; 1996:  $n = 77$  and  $57$ ; 1997:  $n = 74$  and  $58$ ). Wetland availability was expected to have limited influence on wetland reuse patterns and less impact on other estimates of fidelity; indeed, a previously used wetland (natal wetland in 1994) of only one female Mallard offspring was dry in 1995. No reliable measures of wetland quality were available.

Although much less reliable than radio-tracking data (where  $P_d = 1$ ), opportunistic observations of nasal-marked females were also recorded ( $P_d < 1$ ). For individual female parents and female offspring, the index of fidelity was: (number of observations in year  $t$  obtained on previously used wetland in year  $\leq t-1$ /the total number of observations in year  $t$ )  $\times 100$ .

### Statistical Analyses

Statistical tests follow Zar (1984) and analyses were performed using SAS (SAS Institute 1990). A limited set of *a priori* models was created to evaluate hypotheses about variation in wetland fidelity. Wetland reuse (binary response: no, yes) by a given female was modelled with logistic regression (PROC GENMOD), using number of days tracked, species, female status (parent, offspring), distance between successive nests (square root transformed) and percentage of ducklings fledged in the previous year as explanatory variables. The authors began with a global model that included these variables, and then considered simpler models that enabled them to evaluate hypotheses of interest.

The best approximating model(s) was selected using Akaike's Information Criterion adjusted for sample size (hereafter  $AIC_c$ , Burnham & Anderson 1998). Models were compared by determining the difference in  $AIC_c$  between the best model and other models in the candidate set ( $\Delta AIC_c$ ); given low sample size, only models with  $\Delta AIC_c < 1$  are considered in the Discussion (Burnham & Anderson 1998). Seven female Mallard (33% of the total sample) were not radio-marked in consecutive years and were excluded from modelling, as was the single female Mallard offspring, hatched in 1994, that experienced a dry natal wetland when raising a brood in 1995 (details above).

## Results

### Brood survival

Overall, apparent total loss occurred in ~26% of Mallard ( $n = 69$ ) and Gadwall ( $n = 49$ ) broods, and was highest in 1994 in Mallard and in 1996 in Gadwall (**Table 1**). However, after correcting estimates for birds recaptured  $> 6$  weeks after initial marking, adjusted total brood loss was reduced to 17% in Mallard and 14% in Gadwall. Recruited females were detected in six (33%) of 18 Mallard broods and in six (46%) of 13 Gadwall broods where total loss had been declared. Except in 1994, when total loss declined by 27% after accounting for recaptured Mallard, the reduction was ~5% annually. Likewise, when adjusted for recaptures, total loss in Gadwall broods decreased by 18% in 1996 and by 5% in 1997.

**Table 1.** Apparent and adjusted total losses in Mallard *Anas platyrhynchos* and Gadwall *A. strepera* broods, St. Denis National Wildlife Area, Saskatchewan, 1994–1997. Number of reliably tracked broods composed of web-tagged ducklings, apparent percentage (number) of total brood losses during the 30-day radio-tracking period, and adjusted percentage (number) of brood losses after accounting for recaptures of web-tagged ducklings the same year or later are shown.

Year	Species	Broods	Apparent	Adjusted for recaptures <sup>a</sup>	
				Year <i>t</i>	Year ≥ <i>t</i> + 1
1994	Mallard	11	45% (5)	27% (3)	18% (2)
1995	Mallard	15	33% (5)	27% (4)	27% (4)
1996	Mallard	24	17% (4)	17% (4)	12.5% (3)
	Gadwall	28	32% (9)	29% (8)	14% (4)
1997	Mallard	19	21% (4)	21% (4)	16% (3)
	Gadwall	21	19% (4)	19% (4)	14% (3)
All years	Mallard	69	26% (18)	22% (15)	17% (12)
	Gadwall	49	27% (13)	24% (12)	14% (7)

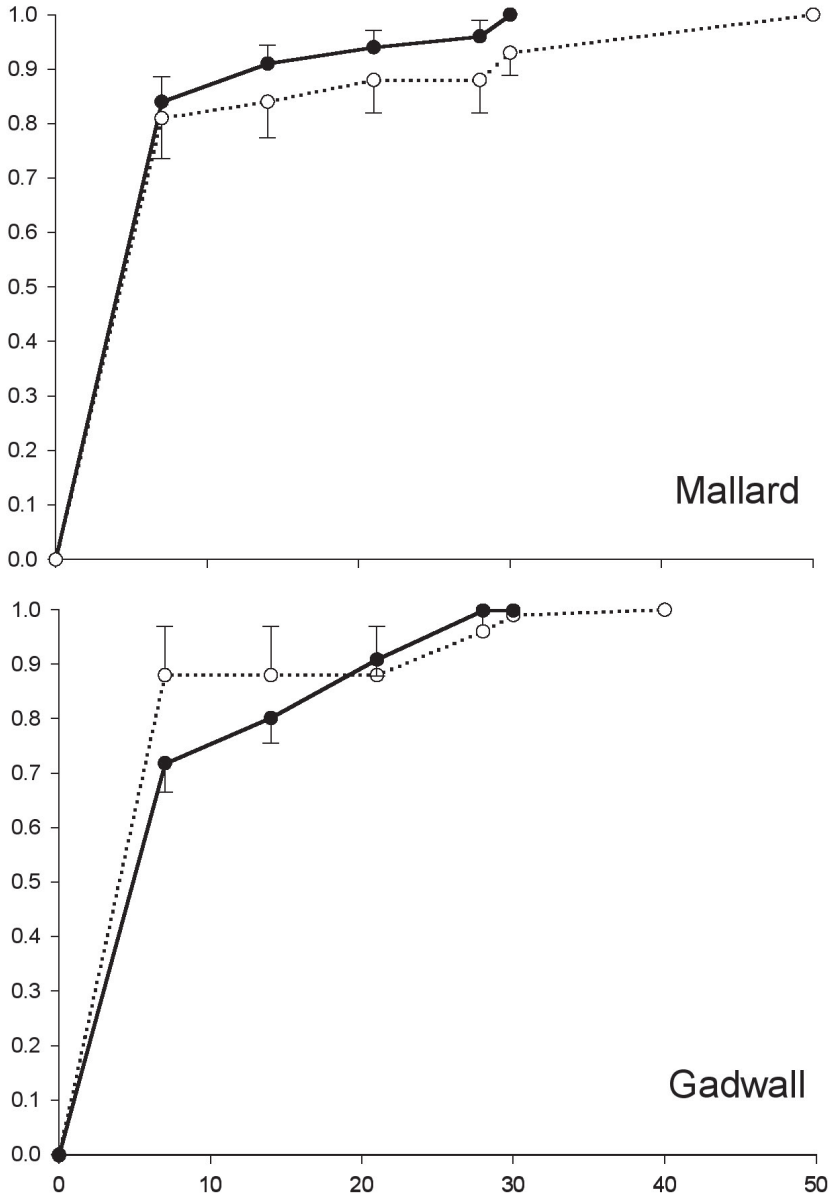
<sup>a</sup>Web-tagged ducklings of both sexes recaptured in bait or drive traps in the same year (Year *t*) or females recaptured dead or alive at nests in a later year (Year ≥ *t* + 1).

Patterns of movement

Excluding wetlands used for < 1 day, the number of movements made by brood-rearing Mallard (median = 2, range = 1–5, *n* = 46) and Gadwall (median = 2, range = 1–5, *n* = 40) was similar. By 30 days after hatching, female Mallard tracked consistently for 50 days (*n* = 15) had moved 93% of the total cumulative distance travelled; after 30 days, female Gadwall (*n* = 8) had travelled > 99% of the total distance moved in 40 days (**Figure 1**). Thus, tracking females for 30 days gave an adequate estimate of distance travelled (hence, wetland use) during brood-rearing.

Brood-site fidelity

Female Mallard radio-tracked in more than one year used from one to five wetlands during brood rearing (median = 3, *n* = 34 female-years) and female Gadwall used one to four (median = 2.5, *n* = 10 female-years). In radio-marked Mallard, 36% of female offspring (5 of 14) and 50% of female parents (6 of 12) reused at least one brood-rearing wetland in a later year. In a smaller sample of Gadwall, most female offspring (75%, *n* = 4) and all female parents (*n* = 3) reused at least one wetland. For Mallard, female offspring spent 2–26 days (mean = 11 days) on wetlands where they had been raised as ducklings, and female parents spent 4–30 days (mean = 15) there; ranges



**Figure 1.** Upper panel: Relative cumulative distances (y-axis) moved overland between wetlands by female Mallard tracked for 30 days in St. Denis National Wildlife Area, Saskatchewan, 1994–1997 (solid line;  $n = 31$ ) versus a maximum of 50 days (broken line;  $n = 15$ ) during brood-rearing. Lower panel: As above, for Gadwall tracked for 30 days ( $n = 40$ ) versus a maximum of 40 days ( $n = 8$ ). Vertical lines represent one standard error.

in Gadwall were 2–21 days for female offspring and 2–7 days for female parents.

To explain variation in wetland reuse, a logistic regression model which incorporated effects of species and status (female parent, female offspring) was the best approximating model ( $AIC_c = 33.320$ ). Based on this model, radio-marked female offspring ( $n = 15$ ) showed weaker wetland fidelity ( $\beta = -1.800 \pm 0.991$  s.e.) than did female parents ( $n = 11$ ), as did Mallard ( $n = 19$ ) when compared ( $\beta = -1.894 \pm 1.240$  s.e.) with Gadwall ( $n = 7$ ). [A status-related difference in wetland reuse was consistent with a contingency table analysis (G-test,  $G = 3.49$ ,  $df = 1$ ,  $P = 0.062$ )]. Other plausible models involved single effects of female status ( $\Delta AIC_c = 0.361$ ), or combined effects of status and distance between successive nests ( $\Delta AIC_c = 0.447$ ;  $\beta = -2.116 \pm 1.048$  s.e. and  $0.064 \pm 0.044$  s.e., respectively). Fidelity was unrelated to previous fledging success or number of days that broods were tracked (**Table 2**). Because the Gadwall sample was smaller, Mallard was looked at separately by repeating all models except those with a 'species' effect. This set of analyses indicated that modelling an effect of female status alone ( $\beta = -1.658 \pm 1.029$  s.e.) was best ( $AIC_c = 28.168$ ), followed by a model ( $\Delta AIC_c = 0.093$ ) that included female status and distance between successive nests ( $\beta = -2.378 \pm 1.121$  s.e. and  $0.079 \pm 0.054$  s.e., respectively).

Using data for all radio-tracked females ( $n = 34$ ), distances from former brood-rearing or natal wetlands to wetlands used one or more years later averaged 2,640 m (s.e. = 354 m,

$t_{32} = 8.40$ ,  $P < 0.001$ ) closer together than distances from previously used wetlands to randomly selected, semi-permanent or permanent wetlands. Likewise, the direction of movements between successively used wetlands was  $38^\circ$  (s.e. =  $16^\circ$ ,  $t_{32} = 2.460$ ,  $P = 0.019$ ) closer together than that of bearings between used and randomly selected wetlands. Finally, females moved an average 556 m (s.e. = 171 m;  $t_{32} = 2.108$ ,  $P = 0.043$ ) farther to a new brood-rearing wetland relative to its nearest suitable neighbouring wetland.

Opportunistic between-year resightings of 35 nasal-marked birds also indicated frequent occurrence of brood-rearing females on previously occupied wetlands. In female parents, the index of fidelity averaged 62.5% (s.d. = 52,  $n = 8$ ) for Mallard and 32% (s.d. = 46,  $n = 11$ ) for Gadwall. In female offspring, an average 72% (s.d. = 44,  $n = 5$ ) of Mallard and 62% (s.d. = 44,  $n = 11$ ) of Gadwall occurred on wetlands where they had been raised as ducklings.

## Discussion

Area and nest site fidelity have been well documented in this and other nesting Mallard and Gadwall populations (e.g. Clark & Shutler 1999; Lokemoen *et al.* 1990) but this study is among the first to quantify *wetland* fidelity in brood-rearing dabbling ducks using a reliable tracking method. Many female Mallard and Gadwall raised broods on their natal wetlands or on wetlands where they had previously raised ducklings. This general pattern was evident in radio-tracking and observational data; differences between the two methods are presumably related to biases



**Table 2.** Characteristics of nest and wetland use and fledging success for brood-rearing Mallard ( $n = 19$ ) and Gadwall ( $n = 7$ ) females that returned to previously used wetlands (fidelity), and those that did not, at St. Denis National Wildlife Area, Saskatchewan, 1994–1997. Median values are shown (range;  $n$ ).

Variable	Wetland fidelity	Not reused
Distance (m) between successive nest sites	138 (4–2133; 16)	39.5 (0–836; 10)
Number of days radio-tracked	30 (4–30; 16)	30 (3–30; 10)
Previous fledging success (%)	73 (0–100; 14)	73 (0–100; 10)

associated with casual observation of nasal-marked birds recorded when preferentially revisiting wetlands where these birds had previously been seen. Because  $P_d$  is  $\sim 1.0$  for females marked with radio transmitters, and females were tracked daily, it is likely that only very short visits to previously used or to new wetlands would have been missed using this method.

Female parents showed greater wetland fidelity than female offspring, as indicated by the study's most reliable information, radio-tracking data. This could arise if older females are better able to gain access to previously used areas or tend to nest closer to previously used wetlands. Alternatively, older, experienced females may simply exhibit greater fidelity to familiar habitat. Leonard *et al.* (1996, p. 871) found that previously successful Canvasback females returned to former brood-rearing wetlands but did not present patterns for unsuccessful females. In this study, weak fidelity was not observed among unsuccessful females, contrary to the prediction that females should move away from areas where they had experienced poor breeding success

(Table 2). Perhaps previous success in an earlier year or being raised on a wetland is the most reliable cue available for assessing habitat quality; presumably, experience with food resources could have a strong effect on wetland fidelity but unfortunately data to evaluate this hypothesis were lacking.

Fidelity was not related to distance between successive nest sites (Table 2), suggesting that females were not reluctant to move broods long distances overland to traditional brood-rearing areas [see Gendron & Clark 2002 for further details]. The impact of overland moves on duckling survival is not certain because most studies have not been able to determine with certainty whether predation on ducklings at wetlands provokes movements or if movements between wetlands produce higher mortality when ducklings are on land (also see Talent *et al.* 1983). When females did not return to previously used wetlands, they often moved much closer to traditional wetlands than was expected by chance. With one exception, females did not switch wetlands because former sites were dry and therefore unavailable, but

annual changes in food abundance and quality, protective vegetation and competitor and predator densities almost certainly occurred (Lindberg & Sedinger 1998; review by Sedinger 1992, p. 121). Likewise, within-year differences in wetland quality may also help to explain why some females ignored wetlands closest to previously used wetlands (i.e. nearest neighbours) when they switched to new brood-rearing sites.

Most studies assume that ducklings die when females are killed or abandon their broods. In three of four years, total brood loss was overestimated by > 5% in Mallard, as found for Gadwall in one of two years (**Table 1**). If ~15% is representative of a correction for brood losses required in these species, duckling survival would be underestimated; the magnitude of this error is not known because it was impossible to determine how many ducklings survived in broods where total loss had been declared. Likewise, it is uncertain whether this overestimate of brood loss is a by-product of capturing and marking birds. Regardless, some researchers have raised legitimate concerns about estimation of bias such as that reported here and discussed the implications for correct interpretation of their results (e.g. Flint *et al.* 1998).

In this study most assumed losses (**Table 1**) occurred in response to brood abandonment (Mallard, 72%; Gadwall, 77%) rather than death of the brood hen. Gendron & Clark (2000) speculated that female abandonment was more frequent when wetland conditions were good because benefits accruing to female parents exceeded costs associated with brood losses,

duckling mortality typically being low when wetlands are abundant (Dzus & Clark 1998; Rotella & Ratti 1992). Thus, it would be very informative to evaluate factors affecting female abandonment and conditions favouring duckling survival in the absence of their female parent.

Results presented here suggest that population structure could extend through groups of closely related females during brood-rearing, similar to patterns described in box-nesting Goldeneyes (Ruusila *et al.* 2000). Opportunistic observations on three and six occasions showed that female parents and female offspring of radio-marked Mallard and Gadwall, respectively, raised broods at the same time and wetland during 1994–1997. These estimates are low, possibly because few adult females survive more than two breeding seasons during periods when wetland conditions are good (Dufour & Clark 2002) and certainly because not all related females rearing broods were radio-tagged. However, these observations suggest that broods inhabiting the same or neighbouring wetlands may be attended by females with shared ancestry, at least during periods or in areas of relatively stable wetland habitat. Furthermore, given that some ducklings survived from broods that lost their female parent, they could have been adopted and raised by a related female. This may be a previously unrecognised benefit, as yet untested, for strong philopatry in Mallard and Gadwall. We encourage further evaluation of the costs and benefits of wetland fidelity by brood-rearing females and their relation with kinship.

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