



EFFECTS OF SPRING BODY CONDITION AND AGE ON REPRODUCTION IN MALLARDS (*ANAS PLATYRHYNCHOS*)

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ABSTRACT.—We explored predictive models relating body condition and age to nesting propensity, timing of nest initiation, clutch size of first nests, aggregated nest survival, hatching success, and timing of hatch in Mallards (*Anas platyrhynchos*). Nesting propensity had a positive linear relationship with body condition, and second-year (SY) females had a lower probability of nesting than after-second-year (ASY) females (84% and 94%, respectively, at average body condition). Females in better body condition initiated nesting ~15 days earlier than those in poor condition, and SY females nested ~4 days later than ASY females at average body condition. Clutch size of first nests exhibited a curvilinear decline with body condition, such that large clutches were characteristic of females in the best condition that nested early. Nest survival and hatching probability were unaffected by body condition. Younger females had somewhat lower nest survival (11%) than older females (14%), which, in combination with renesting effort, resulted in an age difference in hatching probability (22% and 33%, respectively). Females in better condition hatched nests ~15 days earlier than those in poor condition, and SY females hatched nests ~4 days later, on average, than ASY females. Our results indicate that factors influencing the body condition of female Mallards arriving on breeding areas could influence subsequent reproductive investment and success. Condition effects are primarily through the mechanisms of nesting propensity, clutch size, and timing of nest initiation and hatch. Additionally, we provide evidence that Mallards in their first breeding season have lower reproductive potential than older females. Received 2 April 2007, accepted 17 November 2007.

Key words: age, *Anas platyrhynchos*, body condition, Mallard, reproductive investment, reproductive success.

Effets de la condition corporelle printanière et de l'âge sur la reproduction chez *Anas platyrhynchos*

RÉSUMÉ.—Nous avons exploré des modèles prédictifs reliant la condition corporelle et l'âge à la propension de nidification, la chronologie du début de la nidification, la taille des couvées des premiers nids, la survie des nids agrégé, le succès d'éclosion et la chronologie d'éclosion chez *Anas platyrhynchos*. La propension de nidification présentait une relation linéaire positive avec la condition corporelle et les femelles de deuxième année (DA) avaient une probabilité plus faible de nicher que celles de plus de deux ans (PDA) (84% et 94%, respectivement, pour une condition corporelle moyenne). Les femelles en meilleure condition corporelle ont débuté la nidification ~15 jours plus tôt que celles en mauvaise condition et les femelles DA ont niché ~4 jours plus tard que les femelles PDA pour une condition corporelle moyenne. La taille des couvées des premiers nids affichait un déclin curvilinéaire avec la condition corporelle, alors que les grosses couvées étaient caractéristiques des femelles en meilleure condition ayant niché tôt. La survie des nids et la probabilité d'éclosion n'étaient pas affectées par la condition corporelle. La survie des nids des femelles plus jeunes était quelque peu inférieure (11%) à celle des nids des femelles plus âgées (14%) ce qui, en combinaison avec l'effort de renidification, a résulté en une différence d'âge dans la probabilité d'éclosion (22% et 33%, respectivement). Les nids des femelles en meilleure condition ont éclos ~15 jours plus tôt que ceux des femelles en mauvaise condition. Les nids des femelles DA ont éclos ~4 jours plus tard, en moyenne, que ceux des femelles PDA. Nos résultats indiquent que les facteurs influençant la condition corporelle des femelles *A. platyrhynchos* arrivant sur les aires de reproduction peuvent influencer l'investissement et le succès reproducteurs subséquents. Les effets de la condition agissent principalement sur les mécanismes de propension de nidification, la taille des couvées et la chronologie du début de la nidification et de l'éclosion. De plus, nous fournissons des preuves que les femelles dans leur première saison de reproduction chez *A. platyrhynchos* possèdent un potentiel reproducteur plus faible que les femelles plus âgées.

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INDIVIDUAL QUALITY, OFTEN defined as a measure of fat reserves indexed by mass in relation to structural size (see Schultze-Hostedde et al. 2005; hereafter "body condition"), is an important trait known to correlate with survival and reproduction in birds (Martin 1987, Nilsson 1994, Blums et al. 2005). For many Arctic- and temperate-nesting waterfowl species in which reproduction follows spring migration, fat reserves for egg laying and incubation are critical to meeting the needs of this most energetically demanding period in the annual life cycle (Alisauskas and Ankney 1992). Fat reserves are not infinitely advantageous, and individuals must manage a tradeoff between reserves for successful maintenance, reproduction, and predator avoidance (e.g., Stearns 1992, Sandberg and Moore 1996, Rotella et al. 2003).

The relative importance of quality or body condition on reproduction varies by species depending on species-specific life histories. At the extreme, Arctic-nesting Snow Geese (*Chen caerulescens*) reach breeding grounds in spring before abundant food is available and rely heavily on stored energy reserves to meet the energetic demands of egg laying and incubation (Ankney and MacInnes 1978). The effects of body condition on reproductive investment and success of temperate-nesting ducks—though not as pronounced as the effects on Arctic-nesting species—include effects on breeding propensity (Alisauskas and Ankney 1992, Goudie and Jones 2005), onset of egg laying (Pattenden and Boag 1989, Dubovsky and Kaminski 1994), clutch size (Krapu 1981), and continuous egg production when nests are destroyed during laying (Arnold et al. 2002). How body condition influences seasonal reproductive success of temperate-nesting ducks is less well known.

The acquisition and storage of energy for reproduction generally occurs in late winter or early spring prior to breeding (e.g., Whyte et al. 1986, Dubovsky and Kaminski 1994). Factors affecting nutrient acquisition on wintering or migratory staging areas have the potential to influence subsequent reproductive success (e.g., Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Sandberg and Moore 1996, Newton 2006) and, therefore, fitness. However, empirical data from field experiments that support this influence are scant (Newton 2006).

The influence of age on reproduction is generally well known for birds as a group. Typically, reproductive performance improves with age as the result of a number of possible direct and indirect mechanisms (reviewed in Forslund and Pärt 1995). In waterfowl, evidence indicates that older females typically have higher nest propensity, nest earlier within a season, nest more persistently, and lay larger clutches (reviewed in Rohwer 1992, Losito et al. 1995). Mack and Clark (2006), using a sub-sample of our data, reported that older and structurally larger female Mallards had a higher breeding probability than younger and structurally smaller individuals.

Here, we provide data gathered as part of an extensive study of within-season reproductive investment and success for individual female Mallards (*Anas platyrhynchos*) in the prairie-parklands of Canada. The objectives of our analysis were to assess body condition for midcontinent female Mallards at the onset of breeding and to estimate the relationships between body condition, age, and parameters of reproductive investment and success (i.e., nesting propensity, timing of nest initiation, clutch size, aggregated

nesting survival, hatching success, and timing of hatch). Specifically, we predicted that older females and females with high mass in relation to their size would be more likely to nest, initiate nests earlier in the season, have larger initial clutch size, have higher nest survival and hatching probability, and hatch earlier in the season than younger females or females with low mass in relation to their size.

METHODS

Study area.—We examined individual reproductive investment and success of Mallards on 27 study sites in the prairie-parklands of Canada (Fig. 1) from 1993 to 2000. Most of our study sites were located within the Parkland–Boreal Transition Ecoregion; however, four sites were located on the northern fringe of the Mixed Grassland Ecoregion. Three or four study sites (generally 65 km²) were examined each year, and sites moved among years. The primary land use on all sites was production of cereal grains, oilseeds, and forages and pasture (tame and native grasses) for beef cattle. Areas not in agricultural production included wetlands, road and railway rights-of-way, fencelines, and remnant patches of deciduous trees, shrubs, and grasses. Further site description is provided in Devries et al. (2003).

Capture, transmitter attachment, measurement, and tracking.—We decoy-trapped (Sharp and Lokemoen 1987) 66–137 pre-laying female Mallards at each site (total = 2,660) and implanted them with intra-abdominal radiotransmitters (model IMP/150, Telonics, Mesa, Arizona; Olsen et al. 1992, Rotella et al. 1993). Trapping began in early April, within days of the first Mallards arriving on our study sites, and lasted about two weeks. The precise period varied annually, depending on the spring chronology of habitat characteristics and arrival of Mallard pairs.

Body mass (nearest 10 g) was measured with a 1.5-kg Pesola hand-held spring balance, wing chord (nearest 1 mm) was measured from the end of the carpo-metacarpus to the tip of the longest primary, and head length (nearest 1 mm) was measured from the back of the head (occipital) to the tip of the bill (maximum distance). We collected the second greater secondary covert for later classification of female age on the basis of feather characteristics (Krapu et al. 1979; J. H. Devries and R. G. Clark unpubl. data). Age was classified as either second-year (SY; first breeding season) or after-second-year (ASY; second or subsequent breeding season).

We located each female twice daily between 0600 and 1300 hours using vehicle-mounted, null-array antenna systems and triangulation (Kenward 1987). Tracking commenced immediately following radio attachment and continued until nesting ceased, generally in early July. Females that went missing during ground tracking were searched for during extensive road searches and weekly flights using small aircraft within 4 km of study-site boundaries. When a female was located at a fixed location for three consecutive mornings, she was approached on foot to determine her nesting status. In 1993 and 1994, females were flushed at this point to locate the nest; however, from 1995 onward, suspected nest locations were confirmed using hand-held antennae and close triangulation without flushing. Investigators then returned to find the nest in the afternoon, when laying females are typically absent.

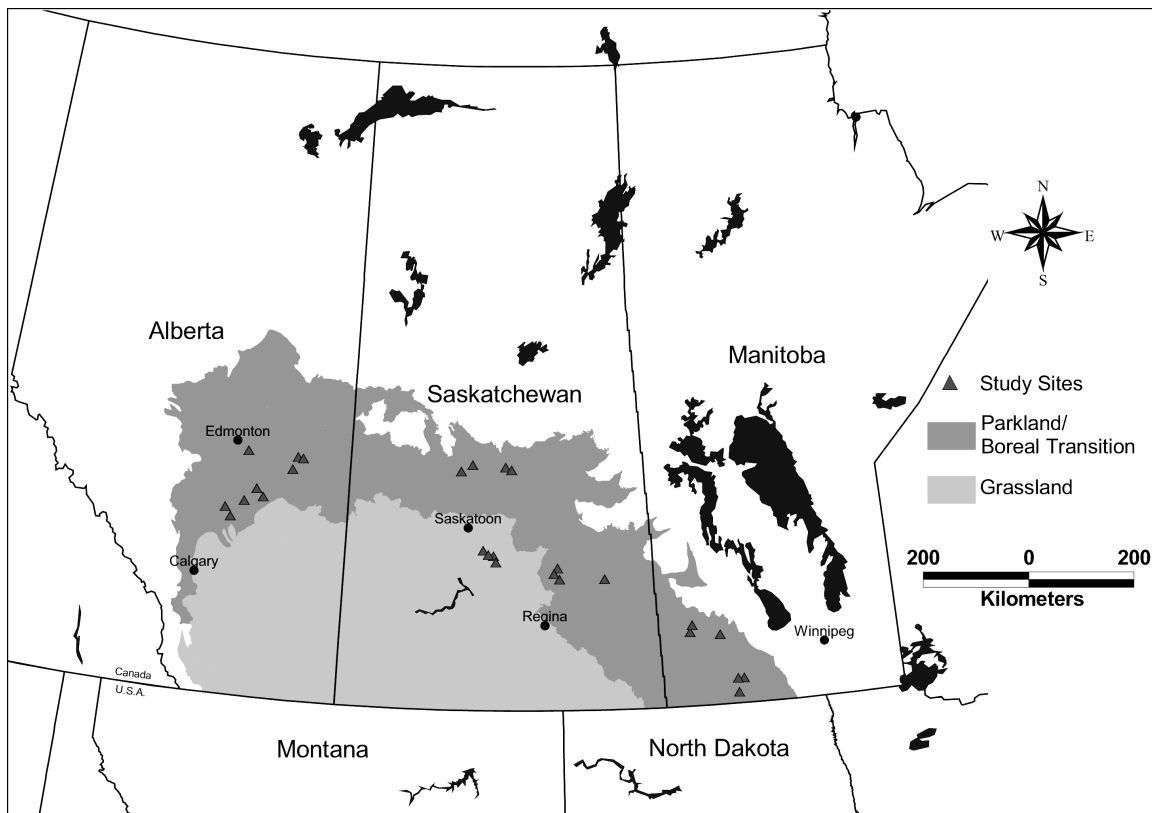


FIG. 1. Study site locations ($n = 27$) in the Parkland–Boreal Transition and Grassland ecoregions of Alberta, Saskatchewan, and Manitoba, where we studied reproductive investment and success of Mallards from 1993 to 2000.

This technique proved effective in reducing investigator-caused abandonment of nests (Thorn et al. 2005), and >90% of nests were found in the laying stage. If a female was absent from the nest for two consecutive telemetry observations, we visited the nest to determine its fate (active, abandoned, hatched, or destroyed; Klett et al. 1986). A nest was determined to be successful if ≥ 1 egg hatched (Klett et al. 1986).

Measures of reproductive investment and success.—Data from radiotagged females were used to estimate various measures of reproductive investment and success, including nesting propensity, timing of nesting, full clutch size of initial nest, aggregate nest survival, hatching success, and timing of hatch. Nesting propensity was defined as the probability of nesting given that a female was resident (i.e., monitored on the study site for >14 days from the date marked to the date last found with telemetry) and survived through the nesting season. Timing of nesting was measured by the initiation date of putative first nests. For first nests found during laying, initiation date was determined by backdating nest age, assuming that one egg is laid per day (Alisauskas and Ankney 1992). For nests found in incubation, we estimated incubation stage by candling (Weller 1956) and backdated to initiation based on the sum of eggs in the bowl and the number of estimated incubation days. In 1993–1994, we measured full clutch size of

first nests by visiting nests on the estimated sixth day of incubation. In subsequent years, to avoid causing nest abandonment, we measured clutch size of first nests at 18 days of incubation. We could not identify nests that may have lost eggs during laying or incubation, so our estimates of full clutch size are assumed. Aggregate nest survival was a female-specific measurement of the survival of all nests initiated by that female as reflected by the ratio of the aggregate days survived to the aggregate days exposed. Hatching success was estimated as the probability that a female hatched a nest within the nesting season. As with nesting propensity, this sample was constrained to resident females that survived the breeding season. Hatch dates for all successful nests were used in analyses of hatch timing.

Body-condition index.—Assuming an allometric relationship between body mass and body size, we estimated body condition as the residuals from an ordinary least-squares (OLS) regression of the log of body mass on an index of body size. The body-size index was calculated as the first principal component (PC1) using PROC PRINCOMP in SAS (SAS Institute 2004) of wing and head length. PC1 accounted for 63% of the overall variation between head and wing measurements. Although much controversy surrounds the calculation and evaluation of methods for estimating body condition (see review in Green 2001), recent analysis suggests that the

OLS method is still superior to alternatives and stands up to criticism (Schulte-Hostedde et al. 2005).

Statistical methods.—To evaluate the relationship between body condition and measures of reproductive investment and success, we developed a set of candidate models to assess each of the reproductive parameters of interest (Appendix). In addition to the body-condition index (BCI), we included other variables in the candidate models that are known to affect reproductive investment and success. We included the random effect of study site (SITE; Rotella et al. 2004) to account for unmeasured variation characterizing individual sites because sites were randomly selected from a population of potential study sites. The effect of female age (AGE) was included to account for variation attributable to female experience and other age-related factors (Forslund and Part 1995). Relative nest-initiation date (IDATE) was included to account for seasonal variation in clutch size (e.g., Cowardin et al. 1985). We standardized nest-initiation and hatch dates for each site-year by subtracting the date of the first nest initiated or hatched from the date of each individual nest initiated or hatched at that site. Nest-initiation dates and hatch dates were $\log + 1$ transformed to improve normality and model fit (IDATE skew = 0.77, $n = 2,102$; hatch-date skew = 0.36, $n = 724$). Despite our intensive tracking efforts, we know that we did not detect all nest initiations for all females and, hence, we included a site-specific nest detection rate (ND) (McPherson et al. 2003) as a site-level correction for this potential bias. To account for the influence of annual habitat condition on reproductive investment (e.g., Piletz et al. 2000), we included a pond index variable (PI) based on the inverse-distance-weighted standardized variation from median pond counts from the nearest three U.S. Fish and Wildlife Service–Canadian Wildlife Service May Breeding Waterfowl Survey transect segments (Benning 1976). Given the spacing of transect segments, three segments were generally within 29 km of all study sites. This variable was included in candidate models as an alternative to SITE. We included the quadratic form of BCI to account for potential curvilinear effects of body condition. We also included first-order interactions in specific candidate models. These included one-way interactions between BCI and AGE, PI, and ND.

We fit all models using generalized nonlinear regression (PROC NLMIXED in SAS). For models where the response variable was binomial (breeding propensity, hatching success), we linked explanatory variables to the response using a logistic function. We tested fit of the global model ($\hat{c} = \text{Pearson } \chi^2 / \text{degrees of freedom}$) for each candidate model set to determine the need for a variance inflation factor (\hat{c}). Because some variables were mutually exclusive, we included BCI, BCI², AGE, SITE, and the BCI*AGE interaction in the global model. We compared models using Akaike's information criterion (AIC; Akaike 1973). Estimates of \hat{c} were <1.49 in all candidate model sets and, therefore, we did not adjust AIC values for variance inflation. We present and rank models within four AIC units of the best-ranking model (Burnham and Anderson 2002). Within this model set, only models structurally equivalent to or simpler than the top-ranked model were considered to be competing and used to draw inferences. We used multimodel inference techniques to average coefficient estimates for variables that appeared in competing models. We used Akaike

weights (w_i) as a measure of support for a particular model being the best model (Burnham and Anderson 2002). We used the ESTIMATE function in PROC NLMIXED to estimate the relationship of BCI to each of the reproductive parameters modeled. Means and parameter estimates are presented \pm SE.

RESULTS

We determined nesting propensity for 2,410 radiomarked female Mallards, many more of which attempted to nest ($n = 2,135$; 89%) than did not ($n = 275$; 11%). The percentage of females not attempting to nest ranged from 3 to 27% when summarized by SITE. Standardized nest-initiation date (mean = 21.0 ± 0.3) was determined for 2,102 putative first nests. We used full-clutch information from 542 females where full clutch was determined for putative first nests. We screened the data to exclude clutch sizes of <7 eggs (probable depredated nests) and >12 eggs (which probably included eggs from more than one female). The mean clutch size was $9.1 (\pm 0.1)$ eggs, and modal clutch size was 9. We determined aggregated nest survival and ultimate hatching success over 4,156 nests generated by 2,100 females. Unsuccessful females ($n = 1,467$; 70%) outnumbered successful females ($n = 633$; 30%). The percentage of females at each site that were unsuccessful ranged from 37 to 85%. Standardized hatch date (mean = 25.4 ± 0.7) was determined for 724 hatched nests.

Nesting propensity.—We considered the top-ranked model to be the only competing model of those within 4 Δ AIC units (Table 1). This model included the variables BCI, AGE, and SITE, received a relative model weight of 0.47, and predicted a positive linear relationship between nesting propensity and BCI ($\hat{\beta} = 3.17 \pm 1.04$; Fig. 2), with lower nesting propensity for SY females (0.84 ± 0.02) than for ASY females (0.94 ± 0.01 ; $\hat{\beta} = 1.14 \pm 0.15$).

Timing of nesting.—We considered two candidate models within 4 Δ AIC units of the most parsimonious model to be competitors explaining variation in timing of nest initiation (Table 1). The top-ranked model indicated an unequivocal negative curvilinear relationship between BCI and relative nest-initiation date, with females in better condition initiating nests earlier (BCI² $\hat{\beta} = -4.03 \pm 2.12$; Fig. 3). The alternative model suggested that the relationship between BCI and timing of nest initiation was linear ($\hat{\beta} = -2.24 \pm 0.24$). Both models included the same AGE effect (mean $\hat{\beta} = -0.20 \pm 0.03$) and indicated that ASY females initiated nests about four days earlier than yearling females at average body condition (ASY = 15.2, 95% confidence interval [CI]: 14.1–16.5; SY = 18.9, 95% CI: 17.3–20.5; Fig. 3). Relative model weights between the curvilinear ($w_i = 0.50$) and linear ($w_i = 0.22$) relationships with body condition lend most support to the former. The best approximating model indicates that females in the best condition nested, on average, 15 days earlier than those in the worst condition.

Clutch size.—Of three models within 4 Δ AIC units of the best approximating model, we considered only the top-ranked model (Table 1). The top-ranked model included the variables IDATE, BCI, BCI², and SITE, and this model received high relative model weight ($w_i = 0.51$). This model indicates that clutch size of first nests declined with nest-initiation date ($\hat{\beta} = -0.41 \pm 0.04$)

TABLE 1. Top-ranked models ($\Delta\text{AIC} < 4.0$) used to evaluate the influence of body condition and age on nesting propensity, relative initiation date, first clutch size, aggregate nest survival, hatching success, and relative hatch date of female Mallards at 27 sites in the prairie-parklands of Canada, 1993–2000. Only models structurally equivalent to or simpler than the top model and within 4 AIC units of the top model were considered for interpretation (in bold).

Response	Model ^a	–2LL ^b	K ^c	ΔAIC^d	w_i^e
Nesting propensity (Minimum AIC = 1,567.6, $\hat{c} = 0.91$)	BCI+AGE+SITE	1,559.6	4	0	0.47
	BCI+AGE+BCI*AGE+ SITE	1,558.8	5	1.20	0.26
	BCI+BCI ² +AGE+SITE	1,559.7	5	2.15	0.16
	BCI+BCI ² +AGE+BCI*AGE+ SITE	1,558.6	6	3.01	0.10
	NULL	1,713.2	1	1,711.19	0.00
Relative nest-initiation date (Minimum AIC = 4,540.2, $\hat{c} = 1.49$)	BCI+BCI²+AGE+SITE	4,528.2	6	0	0.50
	BCI+AGE+SITE	4,531.8	5	1.62	0.22
	BCI+BCI ² +AGE+BCI*AGE+SITE	4,528.2	7	2.00	0.18
	BCI+AGE+BCI*AGE+SITE	4,531.5	6	3.38	0.09
	NULL	4,760.2	1	224.05	0.00
First clutch size (Minimum AIC = 1,513.0, $\hat{c} = 1.26$)	IDATE+BCI+BCI²+SITE	1,501.0	6	0	0.51
	IDATE+BCI+BCI ² +AGE+BCI*AGE+SITE	1,498.9	8	1.98	0.19
	IDATE+BCI+BCI ² +AGE+SITE	1,501.0	7	2.00	0.19
	NULL	1,619.0	1	110.02	0.00
Aggregate nest survival (Minimum AIC = 7,803.0, $\hat{c} = 0.98$)	AGE+SITE	7,797.0	3	0	0.56
	BCI+AGE+SITE	7,796.9	4	1.92	0.21
	BCI+BCI ² +AGE+SITE	7,796.3	5	3.24	0.11
	BCI+AGE+BCI*AGE+SITE	7,796.9	5	3.92	0.08
	NULL	8,143.7	1	342.66	0.00
Hatching success (Minimum AIC = 2,441.6, $\hat{c} = 0.48$)	AGE+SITE	2,435.6	3	0	0.39
	BCI+AGE+SITE	2,434.0	4	0.39	0.32
	BCI+AGE+BCI*AGE+SITE	2,433.8	5	2.25	0.13
	BCI+BCI ² +AGE+SITE	2,434.0	5	2.44	0.12
	NULL	2,568.5	1	128.96	0.00
Relative hatch date (Minimum AIC = 2,160.8, $\hat{c} = 1.11$)	BCI+AGE+SITE	2,150.8	5	0	0.41
	BCI+AGE+BCI*AGE+SITE	2,150.5	6	1.68	0.18
	BCI+AGE+BCI ² +SITE	2,150.5	6	1.75	0.17
	BCI+SITE	2,155.7	4	2.87	0.10
	BCI+AGE+BCI*AGE+BCI ² +SITE	2,149.9	7	3.10	0.09
	NULL	2,197.4	1	40.56	0.00

^aBCI = female body-condition index, SITE = random effect of study site, AGE = female age class, IDATE = site-specific relative nest-initiation date, and NULL = intercept only.

^b–2*Log-likelihood for the listed model.

^cNumber of estimated parameters.

^dThe difference in value between AIC of the most parsimonious model and of the model in question.

^eAkaike model weights reflect the amount of evidence in favor of the model in question given the model set and the data. See Appendix for the full model set.

and declined in a curvilinear form with BCI such that clutch sizes declined with condition at a higher rate in the upper range of body condition than in the lower ranges (Fig. 4). Large clutches are characteristic of females in the best condition initiating the earliest nests.

Aggregate nest survival.—We considered only the most parsimonious model of the four within 4 ΔAIC units to make inferences regarding factors related to aggregate nest survival. This model included only the variables AGE ($\hat{\beta} = 0.15 \pm 0.04$) and SITE and received most of the relative model weight ($w_i = 0.56$; Table 1). However, the estimated aggregate daily survival rate for nests of ASY females ($P = 0.946 \pm 0.004$) was only slightly higher than that for SY females ($P = 0.938 \pm 0.004$).

Hatching success.—As with nest survival, only the most parsimonious model, which included AGE ($\hat{\beta} = 0.53 \pm 0.11$) and SITE, was used to draw inferences regarding covariates related to hatching success (Table 1). This model received moderate relative weight

($w_i = 0.39$) and indicated that the probability of hatch was considerably higher for ASY females ($P = 0.33 \pm 0.03$) than for SY females ($P = 0.22 \pm 0.02$). The addition of a linear BCI effect resulted in comparable model weight ($w_i = 0.32$); however, the BCI effect estimate was equivocal ($\hat{\beta} = 0.93 \pm 0.77$).

Timing of hatch.—The top-ranked model explaining variation in the timing of hatch included the effects of BCI ($\hat{\beta} = -1.68 \pm 0.60$), AGE ($\hat{\beta} = -0.20 \pm 0.09$), and SITE ($w_i = 0.41$; Table 1). A competing model within 4 ΔAIC units included only the effects of BCI ($\hat{\beta} = -2.09 \pm 0.58$) and SITE; however, this model received relatively low weight ($w_i = 0.10$). The top-ranked model indicated a strong negative relationship between relative hatch date and BCI (Fig. 5) such that females in better condition hatched about 15 days earlier. This model also indicated that SY females hatched nests about four days later than ASY females (SY = 19.9, 95% CI: 16.3–24.3; ASY = 16.1, 95% CI: 13.7–19.0; Fig. 5); however, this difference is somewhat equivocal.

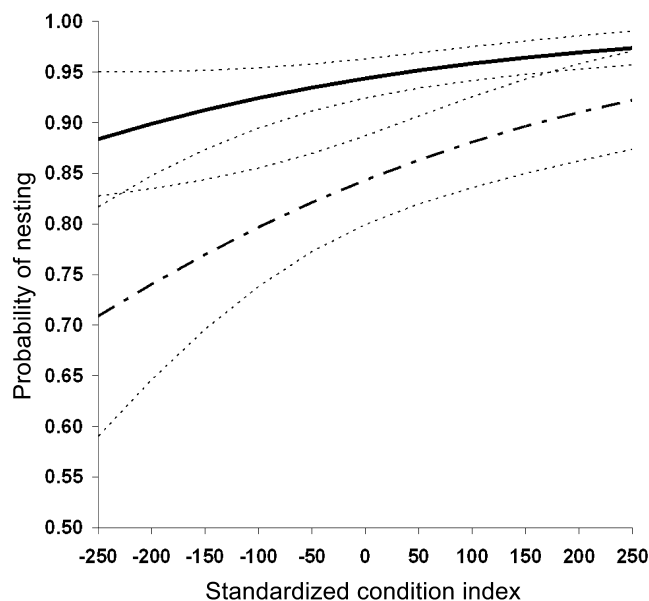


FIG. 2. Predicted probability of nesting (propensity) in relation to arrival body condition for yearling (SY; dashed line \pm 95% confidence interval [CI]) and adult (ASY; solid line \pm 95% CI) female Mallards ($n = 2,410$) captured and radiomarked on 27 study sites in the prairie-parklands of Canada, 1993–2000.

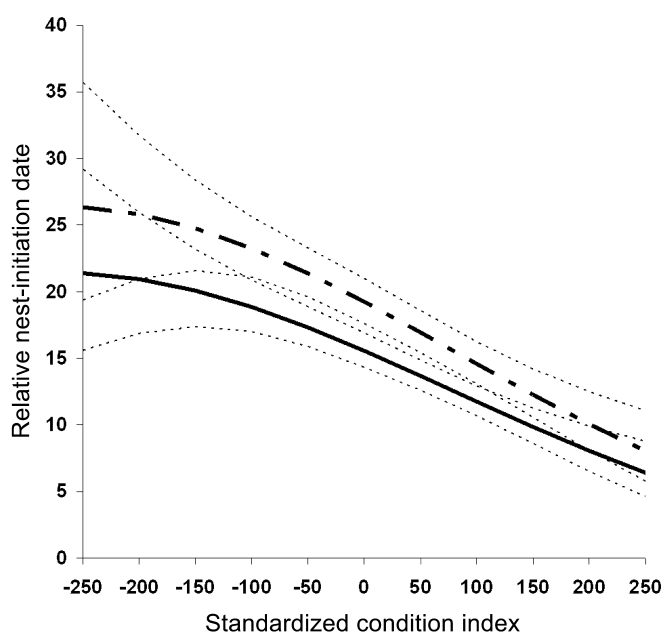


FIG. 3. Predicted nest-initiation date in relation to arrival body condition for yearling (SY; dashed line \pm 95% confidence interval [CI]) and adult (ASY; solid line \pm 95% CI) female Mallards ($n = 2,102$) captured and radiomarked on 27 study sites in the prairie-parklands of Canada, 1993–2000.

DISCUSSION

Previously, Heitmeyer and Fredrickson (1981) drew inferences from correlations between the condition of wetlands on important wintering areas and subsequent population-level Mallard recruitment indices. As a result, they postulated that poor habitat conditions on important wintering areas reduced subsequent reproductive success through bioenergetic mechanisms. Endogenous reserves accumulated in winter, especially late winter, were postulated to allow early breeding by directly augmenting clutch-formation and allowing rapid accumulation of limiting nutrients (e.g., protein) on arrival at the breeding grounds. Supporting evidence that ties female arrival condition to subsequent reproductive success has been lacking. Comparatively, the influence of female age on reproduction has received more attention (Baldassarre and Bolen 2006).

Our objective was to use data from an unprecedented examination of reproductive investment and success of free-ranging female Mallards in prairie Canada to explore the potential for cross-seasonal influences on recruitment. Our results provide new and further evidence that spring body condition and age are correlated with reproductive investment and success in Mallards. Further, we suspect that our estimates are less affected by radio-attachment effects (Rotella et al. 1993, Paquette et al. 1997) that may have limited inference in previous, similar studies (e.g., Cowardin et al. 1985, Losito et al. 1995). We did not collect similar reproductive data for Mallards without transmitters and, hence, we do not know whether a significant transmitter effect is present in our results. A marker effect would bias model results if the effect was related to female age or condition status.

An assumption in our analysis is that our body-mass measurements are a close approximation of arrival body mass unaffected by local nutrient accumulation. Although we recognize some potential for confounding variation, we believe we have come as close as possible to measuring this parameter in a free-ranging population of Mallards by intensive sampling as soon as females arrived on our study areas. Given this assumption, our analysis allows partial separation of age and body-condition effects on reproductive investment and success.

Nesting propensity.—The decision to attempt nesting has obvious implications for reproductive success. Female ducks may not attempt breeding for several reasons, including poor habitat conditions or poor body condition (e.g., Goudie and Jones 2005). A female may be able to meet nutritional requirements for basic metabolic function with stored fat reserves but may not have the nutrients left to meet breeding requirements and will likely forego breeding or abandon her attempt early in the cycle.

Although we observed that female Mallards in relatively better body condition had a higher probability of attempting to nest, we could not evaluate the consequences of future reproductive investment for females that forego breeding. Regardless, we observed that SY and ASY female Mallards in relatively poor body condition were less likely to attempt breeding but still had breeding probabilities >0.60 and >0.80 , respectively. We expected an age-class difference in nesting propensity, because yearling female Mallards sometimes forego breeding (Drilling et al. 2002). Delaying first breeding may be a strategy for increasing lifetime reproductive success, as demonstrated for Common Pochard (*Aythya ferina*; Blums and Clark 2004); however, a similar effect was not demonstrated

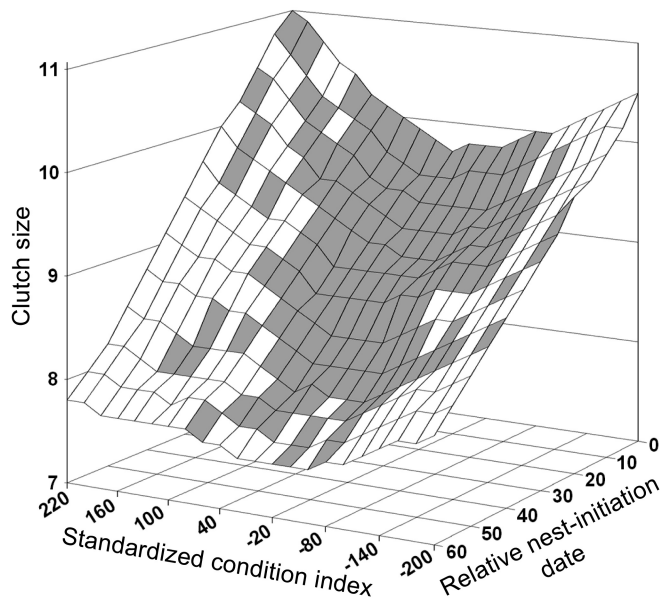


FIG. 4. Predicted clutch size of first nests in relation to arrival body condition and nest-initiation date (standardized) for female Mallards ($n = 542$) captured and radiomarked on 27 study sites in the prairie-parklands of Canada, 1993–2000. The interpolated surface was derived using a spline smoothed fit of the predicted values (shaded cells indicate where data exist) from the best model for clutch size (Table 1).

for Northern Shoveler (*Anas clypeata*) in that study, and the authors suggested that differential survival probability between the species was the mechanism driving this tradeoff. Our estimates of nesting propensity are substantially greater than those of Losito et al. (1995; 0.44 and 0.86, respectively), but we suspect that these differences may be partly attributable to the radio-attachment methods used (Rotella et al. 1993).

Timing of nesting.—For females that attempt to nest, initiation timing has implications for reproductive success. Female Mallards are more likely recruited from early nests than from late ones (Dzus and Clark 1998), and initiation date has consequences for lifetime reproductive success (Drent and Daan 1980, Blums and Clark 2004). Although the influence of body mass or condition on nesting date has been demonstrated in captive Mallards (Pattenden and Boag 1989, Dubovsky and Kaminski 1994), this study is the first, to our knowledge, to document the effect in wild Mallards. Regardless of age class, females that were relatively heavy for their size initiated first nests ~15 days earlier than females in the worst body condition. Tradeoffs likely constrain the timing of nesting; Blums et al. (2005) found evidence of lower survival in the earliest- and latest-nesting females of some European duck species. Although we found that yearling females nested, on average, about four days later than adult females in similar condition, this difference is small and may not be biologically significant. Afton (1984) observed that yearling female Lesser Scaup (*Aythya affinis*) initiated nests five to eight days later than adult females. Cowardin et al. (1985) were unable to detect an age influence on nest-initiation timing in wild Mallards; however, the age influence can be substantial in other duck species (e.g., Hepp and Kenamer 1993).

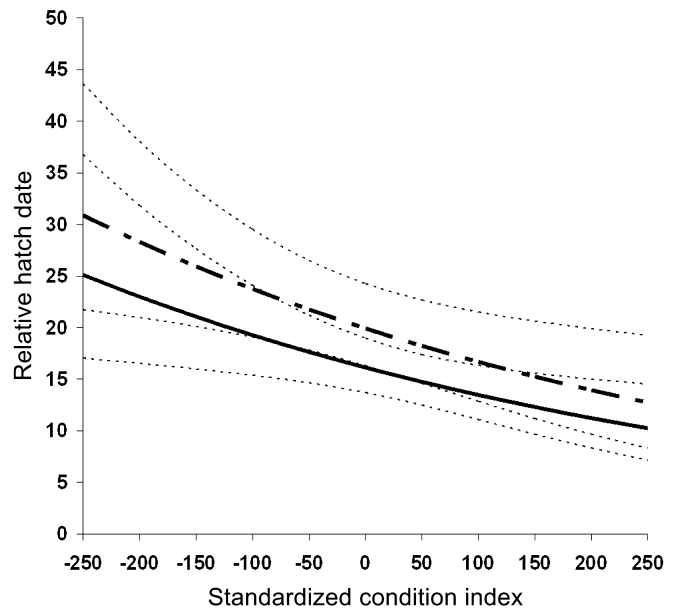


FIG. 5. Predicted hatch date in relation to arrival body condition for yearling (SY; dashed line \pm 95% confidence interval [CI]) and adult (ASY; solid line \pm 95% CI) female Mallards ($n = 724$) captured and radiomarked on 27 study sites in the prairie-parklands of Canada, 1993–2000.

Clutch size.—Our data show that females in the best condition typically produce the largest clutches, after controlling for the initiation-date effect. The decline in clutch size with condition is not linear, which suggests that clutch size is less influenced by condition in the lower half of the condition range. Further, examination of Figure 4 suggests that the effect may be restricted to early nests. We caution that the curvilinear relationship depicted for late nests may be an artifact, given that the nutritional status of these females may be quite different from their arrival condition.

Although there has been much debate in the literature regarding nutrient limitation of clutch size in waterfowl (e.g., Drobney 1991), there is little doubt that temperate-nesting waterfowl use a combination of stored reserves and nutrients acquired locally on breeding areas for clutch formation (Alisauskas and Ankney 1992). Eldridge and Krapu (1988) demonstrated that diet quality affected clutch size to a greater degree than female mass alone. However, Arnold et al. (2002), using our data, demonstrated that some females can sequentially lay ≤ 18 eggs if nests are destroyed in the laying process and that these “continuous layers” were 25 g heavier, on average, than normal laying females. Correlates of female condition, which may include mate quality (e.g., Paulus 1983) facilitating differential access to limited resources (Ashcroft 1976, Hepp 1984), may allow some females to maximize clutch size early, as observed in our data.

As with previous studies (reviewed in Rohwer 1992), our results showed a strong decline in the clutch size of first nests as initiation date increased. Delayed nesting was marginally more prevalent among females in poor arrival condition, which supports

the hypothesis that egg production is costly and may require a threshold of stored reserves (e.g., Reynolds 1972, Rohwer 1992). This pattern may also reflect reduced reproductive investment balancing lower recruitment potential of late-season offspring (Drent and Daan 1980, Rohwer 1992).

Although the review by Rohwer (1992) clearly indicated that in many waterfowl, older females tend to lay larger clutches than yearlings, our data do not support this pattern for Mallards, despite our sample size. Krapu and Doty (1979) found larger clutches for older Mallards in their study, but this pattern was not observed by Cowardin et al. (1985). Hepp and Kenamer (1993) saw no difference in clutch size of Wood Ducks (*Aix sponsa*) with female age, though clutch size increased with age in Lesser Scaup (Afton 1984). Our data suggest that, the individual having made the decision to initiate nesting, factors constraining clutch size in Mallards are similar between age classes.

Aggregate nest survival and hatching success.—Of various population vital rates examined, Mallard population growth rate appears to be most sensitive to nest survival (Hoekman et al. 2002); however, we found that the relationship between body condition and nest survival was trivial. Most Mallard nests initiated on the Canadian prairies are destroyed by predators (Greenwood et al. 1995), an event seemingly unrelated to female body condition. Our data do not support any effect of female condition on nest survival, and this is not surprising, given that effects, if present, would likely be indirect. Our data suggested that nest survival may be lower for SY females than for ASY females (~11% vs. 14%, respectively, when DSR was extrapolated to 35 days); however, this difference is relatively small. Age effects on nest survival have not been reported in many studies to date (but see Afton 1984).

Hatch success, although directly related to nest survival, includes the effect of re-nesting effort and represents a direct measure of annual reproductive success. Arrival body condition does not appear to influence overall hatching probability in Mallards. In our study, nest survival increased as the season progressed in most habitats (Emery et al. 2005). Hence, tradeoffs inherent in the interaction of condition, timing of nesting, and seasonal pattern in nest survival likely smooth hatch probability over all arrival body conditions. Although nest survival was marginally different among age classes, hatch probability was lower for SY than for ASY females (22 vs. 33%, respectively), which indicates somewhat greater nesting effort by ASY females, as has been found previously. A similar age effect on hatch probability was found by Cowardin et al. (1985); however, our estimates are nearly twice those reported for each age class in that study (see table 14 in Cowardin et al. 1985).

Timing of hatch.—The influence of body condition on timing of first nest initiation translates almost directly to timing of hatch. Female Mallards with the lowest BCI are estimated to hatch ~15 days later than females with the highest arrival BCI (Fig. 5). Given previous work examining factors influencing annual and lifetime reproductive success (Blums and Clark 2004), the influence of arrival body condition is likely greatest through the mechanism of hatch timing. Early-hatched nests typically have larger clutch sizes, may be more optimally timed for aquatic food abundance or availability (Haramis 1975, Dzus and Clark 1998), allow higher duckling survival (Krapu et al. 2000), and allow ducklings more time to complete development before fall migration (Hepp et al. 1986, Johnson et al. 1992). Hatching 15 days later than the earliest-hatched nest

has the potential to decrease recruitment probability from ~28% to ~22% (R. G. Clark pers. comm.). Further, females hatching early nests may have increased survival probability (Blums and Clark 2004). Our finding that SY females hatch about four days later, on average, than ASY females, although a relatively small difference, may still result in population-level effects, given the seeming importance of hatch timing.

Our observations generally support the hypothesis that body condition of females arriving at the breeding location can influence subsequent reproduction for a temperate-nesting duck species. Effects are primarily through the mechanism of nesting propensity, clutch size, and the timing of nest initiation and hatch. By extension, factors negatively affecting the body condition of females arriving on breeding areas could reduce subsequent population-growth rates. Drought, adverse weather, change in agricultural practices, or changes in habitat availability in North American wintering and migratory staging sites are some factors that could affect the body condition of wintering and staging ducks. These factors may lead to density-dependent population responses, given spatial and temporal influences on population distribution. Understanding how these extrinsic factors influence body condition could help integrate models for managing Mallard populations during both the breeding and nonbreeding seasons.

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APPENDIX. Candidate models used to assess variation in the reproductive parameters of female Mallards.

Model ^a	Nesting propensity	Relative initiation date	Clutch size ^b	Aggregate nest survival	Hatching success	Relative hatch date
NULL	X	X	X	X	X	X
SITE	X	X	X	X	X	X
BCI SITE	X	X	X	X	X	X
AGE SITE	X	X	X	X	X	X
BCI BCI ² SITE	X	X	X	X	X	X
AGE BCI SITE	X	X	X	X	X	X
BCI BCI ² AGE SITE	X	X	X	X	X	X
BCI AGE BCI*AGE SITE	X	X	X	X	X	X
BCI BCI ² AGE BCI*AGE SITE	X	X	X	X	X	X
BCI PI	X	X	X	X	X	X
BCI BCI ² PI	X	X	X	X	X	X
BCI PI BCI*PI	X	X	X	X	X	X
BCI BCI ² PI BCI*PI	X	X	X	X	X	X
BCI PI AGE	X	X	X	X	X	X
BCI BCI ² PI AGE	X	X	X	X	X	X
BCI PI AGE BCI*AGE	X	X	X	X	X	X
BCI BCI ² PI AGE BCI*AGE	X	X	X	X	X	X
BCI PI AGE AGE*PI	X	X	X	X	X	X
BCI BCI ² PI AGE AGE*PI	X	X	X	X	X	X
BCI ND	X	X				X
BCI BCI ² ND	X	X				X
BCI ND BCI*ND	X	X				X
BCI BCI ² ND BCI*ND	X	X				X
BCI ND AGE	X	X				X
BCI BCI ² ND AGE	X	X				X
BCI ND AGE BCI*AGE	X	X				X
BCI BCI ² ND AGE BCI*AGE	X	X				X
BCI ND AGE ND*AGE	X	X				X
BCI BCI ² ND AGE ND*AGE	X	X				X
BCI ND PI	X	X				X
BCI BCI ² ND PI	X	X				X
BCI ND PI BCI*ND	X	X				X
BCI ND PI BCI*PI	X	X				X
BCI ND PI AGE	X	X				X
BCI ND PI AGE BCI*AGE	X	X				X
BCI ND PI AGE ND*AGE	X	X				X
BCI ND PI ND*PI	X	X				X
BCI ND PI AGE ND*PI	X	X				X
BCI BCI ² AGE ND PI ND*PI	X	X				X

^aBCI = female body-condition index, SITE = random effect of study site, AGE = female age class, PI = site-specific pond-abundance index, and ND = site-specific nest-detection rate, NULL = intercept only.

^bEvery model except null included a relative-initiation-date variable (IDATE).