

Body mass, energetic constraints, and duck nesting ecology

Dave Shutler, Mark L. Gloutney, and Robert G. Clark

Abstract: Body size can impose tighter energetic constraints on smaller than on larger species. Accordingly, we tested whether smaller duck species were more inclined than larger species to save on metabolic costs by using nest sites that received more solar radiation (insolation) and experienced higher temperatures, and by initiating nests during warmer seasons. We also tested whether smaller duck species nested closer to food (wetlands) than did larger species, to save energy during incubation or on foraging trips. Because nest sites receiving less insolation may also be less concealed, we made an additional prediction that nest-predation rates would be higher for smaller than for larger species. Tests were also conducted intraspecifically. Over 8 years, variables used for testing these predictions were quantified at nests representing six species and 838 individuals. Body masses of 189 females from these nests were also obtained. Predictions that body size would affect nest concealment, nest-initiation date, and distance from water were supported by the results of interspecific tests. Additional support for the prediction that smaller species would nest later in the year was obtained from the literature. The prediction that species using less nest concealment would also have higher predation rates was not supported. Intraspecific variation in body mass was not a good predictor of either nest concealment, distance to water, or susceptibility to predation. Overall, our results reveal important influences of body size on duck nesting ecology.

Résumé : La taille peut imposer des contraintes énergétiques plus sévères chez les petites que chez les grosses espèces. Dans cette optique, nous avons cherché à déterminer si les petites espèces de canards sont plus susceptibles que les grosses de réduire leurs coûts métaboliques en construisant leurs nids à des endroits plus exposés aux radiations solaires (ensoleillement) et où les températures sont plus élevées et en nichant au cours de périodes plus chaudes. Nous avons également examiné si les petites espèces de canards nichent plus près de leur source de nourriture (zones humides), économisant ainsi de l'énergie lors de leurs excursions de quête de nourriture pendant l'incubation. Comme les sites des nids qui reçoivent moins d'ensoleillement sont susceptibles d'être moins bien protégés, nous avons considéré une prédiction additionnelle selon laquelle les taux de prédation au nid seraient plus élevés dans le cas des petites espèces. Nous avons également procédé à des tests intraspécifiques. Sur une période de 8 ans, les variables utilisées pour tester les hypothèses ont été quantifiées dans des nids représentant six espèces et 838 oiseaux. La masse a été mesurée chez 189 femelles dans ces nids. Les prédictions selon lesquelles la taille influence le camouflage du nid, la date de construction du nid et sa distance de l'eau ont été vérifiées au cours des tests interspécifiques. L'hypothèse selon laquelle les petites espèces risquent de nicher plus tard dans l'année a également été vérifiée par les données de la littérature. L'hypothèse selon laquelle les espèces dont les nids sont moins bien cachés sont victimes de taux de prédation plus élevés n'a pas été confirmée. La variation intraspécifique de la masse ne s'est pas avérée un bon indicateur du camouflage des nids, de leur distance de l'eau ou de leur susceptibilité à la prédation. Dans l'ensemble, nos résultats révèlent une importante influence de la taille sur l'écologie de la nidification chez les canards.

[Traduit par la Rédaction]

Received March 6, 1998. Accepted May 29, 1998.

D. Shutler,¹ M.L. Gloutney,² and R.G. Clark.³ Canadian Wildlife Service, Prairie and Northern Wildlife Research Centre, 115 Perimeter Road, Saskatoon, SK S7N 0X4, Canada, and the Department of Biology, University of Saskatchewan, 112 Science Place, Saskatoon, SK S7N 5E2, Canada.

¹Author to whom all correspondence should be sent at the following address: Biology Department, Acadia University, 24 University Avenue, Wolfville, NS B0P 1X0, Canada (e-mail: dave.shutler@acadiau.ca).

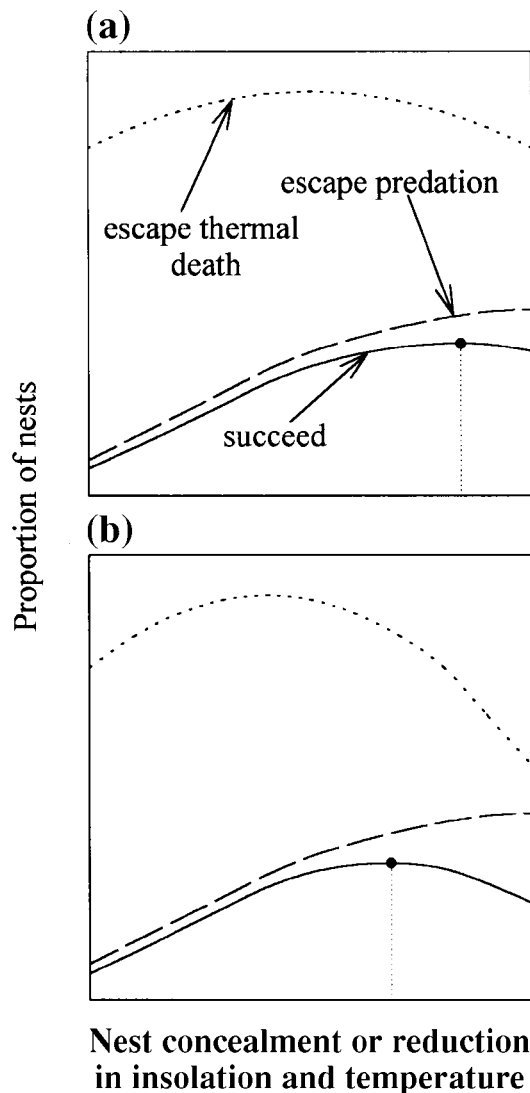
²Present address: Ducks Unlimited, P.O. Box 430, No. 64, Highway 6, Amherst, NS B4H 3Z3, Canada (e-mail: m_gloutney@ducks.ca).

³E-mail: bob.clark@ec.gc.ca.

Introduction

Because of the importance of predation to avian nest survival (Lack 1968; Ricklefs 1969; Martin 1988, 1992, 1996), other factors affecting nesting ecology have received less attention. Among waterfowl species, variation occurs in the amount of solar radiation (insolation) received by nest sites (Gloutney and Clark 1997), time of year in which nesting occurs (Hochbaum 1944; Sows 1955; Keith 1961; Murton and Westwood 1977; Hammond and Johnson 1984; Greenwood et al. 1995), frequency of incubation recesses (Afton 1980; Afton and Paulus 1992; Gloutney et al. 1993), and distance of nests from wetlands (Keith 1961; Livezey 1981a). It has been surmised that some of this variation in nesting ecology arises from interspecific differences in body mass; for example, smaller species may nest in warmer micro-

Fig. 1. Conceptual model of trade-offs among concealment, predation, and thermal environment for large species (a) and small species (b). Increasing concealment provides diminishing antipredator benefits (broken line), and thermal neutrality occurs over a smaller range and has a higher median value for smaller than for larger species (dotted line). Chance of escaping predation and chance of thermal death have multiplicative effects on probability of success (solid line). Optimal concealment (indicated by a point and drop line) is greater for large than for small species.



climates to save on their relatively higher metabolic costs (e.g., Collias and Collias 1984, p. 102; Afton and Paulus 1992; Gloutney and Clark 1997). However, few formal tests of the importance of body mass to nesting ecology have been performed (but see Afton and Paulus 1992; Gloutney 1996; Gloutney and Clark 1997). Herein, we test whether body mass of six species of ducks (blue-winged teal, *Anas discors*; northern shoveler, *A. clypeata*; American wigeon, *A. americana*; northern pintail, *A. acuta*; gadwall, *A. strepera*; and mallard, *A. platyrhynchos*) is related to variation in their nesting ecology.

Females of our focal species differ substantially in body size (late-incubation body masses are 311, 469, 574, 612, 639, and 811 g for blue-winged teal, northern shoveler, American wigeon, northern pintail, gadwall, and mallard, respectively; Duncan 1987a; Forbes et al. 1994). Smaller body size increases the mass-specific metabolic rate and decreases the capacity for storing energy (Peters 1983; Schmidt-Nielsen 1984; Blem 1990; Ankney and Alisauskas 1991). Hence, we expect greater metabolic constraints for smaller species, especially during incubation, when foraging and incubation times conflict (Hogan 1989; Gloutney et al. 1993). For nesting ducks, one potential strategy for dealing with metabolic constraints is to choose nest sites that minimize costs of incubation. In temperate areas, where ambient temperatures are often below thermal neutrality during the nesting season, one strategy may be to select nest sites that experience greater insolation, and hence higher temperatures (Walsberg 1981, 1985; Marzluff 1988; Wolf and Walsberg 1996; Gloutney and Clark 1997; cf. Stokes and Boersma 1998).

Nest sites receiving greater insolation may provide less vegetative concealment (Geiger 1959; Archibold et al. 1996). This could necessitate a trade-off (Marzluff 1988), because nests fail most often because of predation (Lack 1968; Ricklefs 1969; Martin 1996), and nest concealment is the most commonly cited defense against predators (Martin 1992). As an illustration of how body size could influence trade-offs between predation risk and nest microclimate, consider the following conceptual model. First, assume that an increase in nest concealment reduces predation (Fig. 1), but with diminishing returns (Sugden and Beyersbergen 1986). Second, nest abandonment or embryonic death occurs at nest sites that are too cold or too hot (resulting, in either case, in "thermal death" of embryos). Third, thermal neutrality occurs over a smaller temperature range and has a higher median value for smaller than for larger species (Schmidt-Nielsen 1984), which translates into smaller species preferring nest sites with more insolation and potentially less concealment. Fourth, the relationship between predation risk and concealment is the same irrespective of interspecific differences in body size. Risks of failure are multiplicative in determining the probability of nest success. Hence, if a nest with a given level of concealment has a 40% chance of escaping predators and a 90% chance of escaping thermal death of embryos, that nest has a 36% chance of surviving. This model predicts that nest sites will provide less concealment for smaller than for larger species (Fig. 1). In addition, the model predicts that smaller species' nest sites are more likely than those of larger species to occur within the zone of thermal neutrality. Finally, this conceptual model predicts that a greater proportion of nests of smaller species will be depredated.

Aside from choosing an appropriate microclimate for minimizing metabolic costs, ducks may also choose an appropriate macroclimate by adjusting seasonal timing of migration and nesting (predicted by Calder and King 1974, p. 384; Bluhm 1992, p. 334). Trade-offs here include fewer days remaining for reneating, and reduced time available for young to develop prior to southward migration (considered from an intraspecific perspective in Rohwer 1992). To some extent these trade-offs may be balanced by shorter incubation and

development times for smaller species (Gloutney and Clark 1997).

To meet the energetic demands of incubation (Gloutney et al. 1996), smaller species take more frequent nest recesses to forage on wetlands (Afton and Paulus 1992; Gloutney et al. 1993). The necessity for more frequent foraging trips would increase the value of being close to resources (Charnov 1976), which could translate into smaller species nesting closer to water. Alternatively, smaller species may nest closer to water because of allometric relationships affecting travel efficiency of ducklings. However, the costs of this single duckling trip may be insubstantial within the range of distances from wetlands where ducks nest (Duncan 1987*b*). In any case, if preference for proximity to wetlands concentrates nests sufficiently, it could further increase predation rates on nests of smaller species.

We used 8 years of data (1983–1990) describing, for six species of ducks, nest concealment (using two different measures of vertical occlusion and one measure of vegetation height), initiation date, proximity to wetlands, and fate. From 1990 to 1992, we also recorded insolation and temperatures at random non-nest sites at which we measured vegetation height. We tested predictions that smaller species would (i) use nest sites with less concealment and higher insolation, (ii) nest later in the year, (iii) nest closer to wetlands, and (iv) incur higher nest-predation rates than larger species. Using body masses of females captured at nests, we tested intraspecifically predictions *i*, *iii*, and *iv*. We also reviewed the literature to broaden our test of prediction *ii*.

Study area and methods

The study area was the 385-ha St. Denis National Wildlife Area in Saskatchewan, Canada (described in Sugden and Beyersbergen 1985). Duck nests were found in each year during 3 or 4 systematic searches of the entire study area (except cropland, which makes up about 37% of the total area and in which ducks rarely nest; R.G. Clark, unpublished data). Searches were conducted daily between 07:00 and 15:00 from early May to mid-July in 1983–1990 (Gloutney et al. 1993). Species were identified by watching females as they flushed from nests, and by species-typing eggs in, and breast feathers lining, nests (Klett et al. 1986). Dates of nest initiation were estimated by counting the eggs (assuming that one egg was laid per day, and that no eggs were lost) and candling to assess the stage of embryo development (Weller 1956). The date of the first nest initiation of the year (always by a mallard) was assigned a value of zero, and for remaining nests, the relative initiation date was the number of days elapsed since the first nest was initiated. Relative initiation date was used to control for annual variation in dates of nest initiation (see below).

Using candling data for stage of embryo development, capture of females at their nests was timed to be carried out towards the last 2 days of incubation (details in Clark and Shutler 1999). Females are less likely to abandon nests if captured at this stage (Montgomerie and Weatherhead 1988). Body mass to the nearest 5 g was measured on these females.

Following hatch, depredation, or abandonment (for criteria see Klett et al. 1986), vertical concealment was measured in three ways at each nest. First, concealment, i.e., percent occlusion of the nest bowl, was measured as the average percentage of five 6.5-cm² squares on a cardboard disc that was occluded in the vertical plane when viewed from 1 m above the nest bowl. Second, from 1984 on, vegetation height, i.e., the average maximum vegetation height

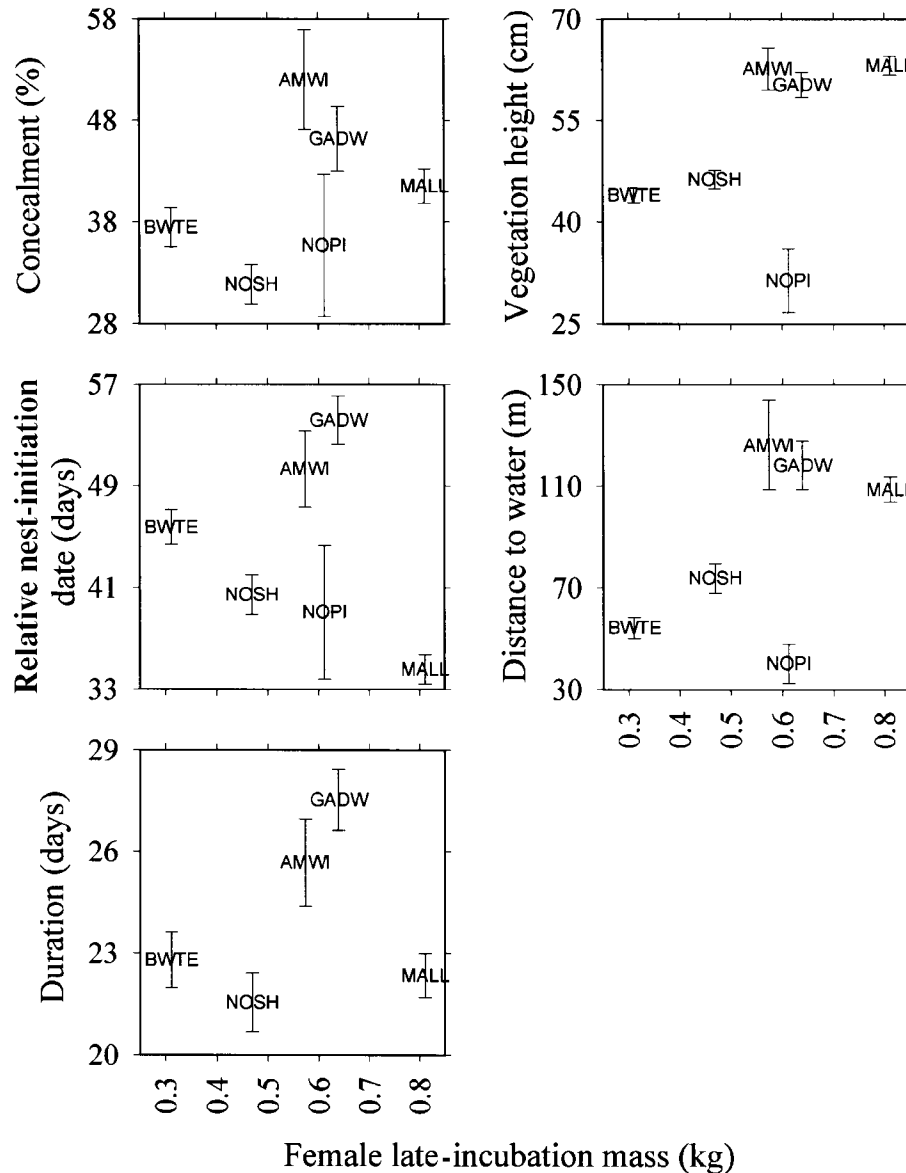
within a 20-cm radius of the nest bowl, was measured with a metre stick or tape measure and integrated by eye. Third, from 1984 to 1986 only, a camera with a 17-mm fisheye lens (170° field of view) was used to take photographs from nest bowls (following Burger 1972), with the top of the camera directed north. A grid was used to divide the photographs into 4 quadrants and, within these quadrants, 10 equal-sized areas were scored on a 10-point scale (9 indicated complete occlusion). Scores for the 10 areas within a quadrant were summed to produce 4 “directional concealment” measures (north concealment, east concealment, etc.). Distance to water was computed to the nearest flooded wetland using maps of the study area. Duration was recorded as the number of days that nests survived, using Johnson’s (1979) assumption that predation events at nests occurred two-fifths of the way through the period between nest visits, and adding the number of days that the nest had survived up to that point.

We assumed that greater concealment and taller vegetation would result in cooler thermal environments at nests. To test this prediction more precisely, during the nesting seasons of 1991–1993, 95 random non-nest sites were set up for the purpose of measuring temperature and insolation across a range of vegetation heights. The combined effects of air temperature and insolation provide a more complete description of animals’ thermal environments (McArthur 1990; Walsberg 1992). Temperature ($\pm 0.1^\circ\text{C}$) and insolation ($\pm 3\%$, W/m^{-2}) were measured using Campbell Scientific 21X dataloggers equipped with CSI 207 temperature/relative humidity probes and LI200S Licor pyranometers (for details see Gloutney and Clark 1997). Dataloggers recorded 30-min means based on 5-s measurement intervals; the 30-min means were used to calculate daily means. Vegetation heights ranged from 10 cm in grasslands to 1000 cm in aspen bluffs. Because temperatures are most often below thermal neutrality from evening to midmorning (Gloutney and Clark 1997), we predicted that east and west concealment would be less for smaller than for larger species, even though concealment in the other cardinal directions may also be less for smaller species (also see Walsberg 1981). The remaining predictions were that smaller species would have later relative initiation dates, shorter distances to water, and shorter durations.

Statistical analyses were performed using SAS Institute Inc. (1989). To create normal distributions, prior to analyses, concealment was arcsine square root transformed and vegetation height was square root transformed. The remaining variables did not require transformation (normality was assessed with Wilk–Shapiro tests). The first set of tests were at the interspecific level, so we wanted each species to have the same weight in analyses. So that each species contributed equally, observations were weighted by the inverse of that species’ sample size. The importance of body mass was simultaneously tested against each of the response variables using multiple analysis of variance (MANOVA). Analysis 1 covered 1984–1990 and used species-specific body mass (Duncan 1987*a*; Forbes et al. 1994) as the explanatory variable and concealment, vegetation height, distance to water, relative initiation date, and duration as response variables. Analysis 2 used data only from 1984 to 1986 but substituted the 4 directional concealment measures for concealment. Although we had data from 16 northern pintail nests, we had only 3 at which vegetation height was measured. Hence, in order to include pintails, analysis 3 was run without vegetation height; this also allowed the use of data from 1983 because vegetation height was not measured that year. Interspecific tests using analyses 1–3 were repeated with actual body masses of females that had been captured at nests.

It was not possible to test whether intraspecific variation in body mass was related to intraspecific variation in nest-initiation date because many females were not captured at their first nest of the year, i.e., females captured later were more likely to be re-nesting. Thus, in intraspecific tests using analyses 1–3, relative

Fig. 2. Relationship between female body mass and five variables relating to nesting ecology (mean \pm SE). BWTE, blue-winged teal; NOSH, northern shoveler; AMWI, American wigeon; NOPI, northern pintail; GADW, gadwall; MALL, mallard. There were no data on duration for northern pintails.



initiation date was now an explanatory variable to control for seasonal variation in female body mass.

Of the nest measures in this study, only nest-initiation dates are commonly reported in the literature. Data from the literature were used to test whether a relationship between body mass and nest-initiation date was a general pattern for waterfowl in other locations. Studies were chosen provided they had measures of central tendency (preferably the mean) for nest-initiation dates of at least two species. Using the same justification as above, so that each species contributed equally to analyses, species were weighted by the inverse of the number of literature reports found for them. Study-specific body masses were not available, so body mass measures were obtained instead from Lack (1968). This analysis had date (1 = 1 January) as the response variable, body mass as the explanatory variable, and foraging niche (surface-feeding "dabbler" or underwater-feeding "non-dabbler") and publication source as class variables, and the interaction between body mass and foraging niche.

Results

We collected 755 days of data on mean daily insolation and temperature from dataloggers at the 95 random non-nest sites. To avoid pseudoreplication from sampling on multiple days at a site, we used a nested ANOVA with date nested within site. Less insolation reached the ground in taller vegetation (canopy height, $F_{[1]} = 147.2$, $P < 0.0001$; date, $F_{[1]} = 4.7$, $P = 0.03$; date nested within site, $F_{[94]} = 16.9$, $P < 0.0001$). Because the smaller ducks rarely nested in aspen bluffs (Clark and Shutler 1999), we repeated the analysis using only the other habitats (699 days from 87 sites); the relationship was essentially unchanged (canopy height, $F = 187.6$, $P < 0.0001$; date, $F = 6.4$, $P = 0.01$; date nested within site, $F_{[86]} = 15.0$, $P < 0.0001$). Average temperature was also lower in taller vegetation, but not significantly so

Table 1. Interspecific relationships between species-specific body mass and variables related to nesting ecology, based on three separate MANOVAs.

Variable (all 1 df)	Analysis 1		Analysis 2		Analysis 3	
	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²	<i>F</i>	<i>R</i> ²
Concealment	3.0	0.00	—	—	4.2	0.01*
Vegetation height	84.2	0.12***	43.6	0.12***	—	—
North concealment	—	—	9.1	0.03**	—	—
East concealment	—	—	8.6	0.03**	—	—
South concealment	—	—	11.1	0.03***	—	—
West concealment	—	—	5.1	0.02*	—	—
Relative initiation date	-18.3	0.03***	-0.6	0.00	-12.9	0.02***
Distance to water	38.3	0.06***	21.9	0.07***	43.1	0.05***
Duration	0.1	0.00	0.7	0.00	—	—
MANOVA result						
Wilks' λ	33.5***		9.3***		23.4***	
df	5		8		3	
Sample size						
Mallards	270		117		342	
Blue-winged teal	134		90		174	
Northern shovelers	119		66		164	
American wigeon	42		19		46	
Gadwall	77		20		96	
Northern pintails	—		—		16	

Note: Negative *F* values from ANOVAs indicate negative correlations with species body mass. Species means for some variables are shown in Fig. 2. Variables or species not included in an analysis are indicated by a dash.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

(canopy height, $F = 3.1$, $P = 0.08$; date, $F = 6.6$, $P = 0.01$; date nested within site, $F = 6.5$, $P < 0.0001$). However, when aspen bluffs were excluded, lower temperatures were observed in taller vegetation (canopy height, $F = 12.4$, $P = 0.0005$; date, $F = 13.7$, $P = 0.0002$; date nested within site, $F = 7.2$, $P < 0.0001$). Collectively, these results indicate that environments were cooler at nests in taller vegetation, although some of these differences may have been offset by reductions in wind speed caused by taller vegetation.

Interspecifically, the raw data suggested that several aspects of nesting ecology are related to body mass (Fig. 2), and many of these univariate relationships held in the multivariate analyses. First, smaller species had less concealment than larger species (analysis 3; Table 1). There was also strong evidence that smaller species nested in shorter vegetation; body mass explained more variation (R^2) in vegetation height than any other variable (Table 1). Smaller species also had less directional concealment at their nest sites (analysis 2). We predicted that the difference between smaller and larger species would be greatest for east and west concealment; trends were opposite to predictions, although not significantly so (F -ratio tests, all P values > 0.50). Smaller species also nested later in the year (except according to analysis 2), and closer to water. However, in no analysis did smaller species suffer higher nest-predation rates (duration in Fig. 2, Table 1). Interspecific tests in which we used actual body mass showed trends in the same direction as the preceding analyses, and R^2 values were similar. However, because of smaller sample sizes, fewer variables were significant. For brevity, we do not present these results.

Intraspecifically, body mass was of limited importance in influencing nesting ecology; only 1 of 12 analyses was sig-

nificant (Wilks' λ values in Table 2), and would not have been so after Bonferroni correction (Rice 1989). None of 10 analyses showed that nest concealment was related to body mass, none of 7 analyses showed that vegetation height was related to body mass, only 2 of 8 analyses showed that directional concealment was related to body mass, and none of 12 analyses showed that distance to water was related to body mass. Finally, none of 12 analyses showed that duration was related to body mass (Table 2).

Eight published sources were used to test the geographic generality of an interspecific relationship between nest-initiation date and body mass (Table 3). The relationship between nest-initiation date and body mass was similar for dabblers and non-dabblers (mass \times foraging niche, $F = 1.0$, $P = 0.33$). After the interaction term was dropped (Alisauskas and Ankney 1994; Sorci et al. 1996), the analysis explained 83% of the variation in nest-initiation date. There was significant variation between dabblers and non-dabblers in nest-initiation date (foraging niche, $F = 19.9$, $P = 0.0001$), non-dabblers having the same body mass as dabblers tending to nest later in the year (Fig. 3). In addition, nest-initiation dates varied geographically (publication source, $F = 19.5$, $P < 0.0001$). After these were controlled for, heavier ducks tended to nest earlier in the year (Fig. 3; $F = 7.3$, $P = 0.01$).

Discussion

We obtained strong support for the hypothesized relationships between body mass and nesting ecology. Our first finding was that smaller species chose nest sites in shorter vegetation and, to some extent, with less vertical concealment. We also showed that sites with shorter vegetation re-

Table 2. Intraspecific relationships between actual body mass and variables related to nesting ecology.

	Mallard	Blue-winged teal	Northern shoveler	American wigeon	Gadwall
Analysis 1					
Variable					
Concealment	2.7	2.2	1.9	-1.7	-0.3
Vegetation height	-2.5	-0.1	5.3*	3.4	0.1
Distance to water	2.0	0.0	1.2	0.3	-0.9
Duration	-0.6	0.1	3.7	-0.1	-0.2
MANOVA result					
Wilks' λ , 4 df	2.6*	0.5	2.4	2.0	0.3
<i>n</i>	62	48	33	19	27
Analysis 2					
Variable					
Vegetation height	-1.2	-0.1	—	—	—
North concealment	2.5	6.0*	—	—	—
East concealment	0.8	6.7*	—	—	—
South concealment	1.8	0.3	—	—	—
West concealment	3.6	0.3	—	—	—
Distance to water	2.8	-0.7	—	—	—
Duration	-1.1	-0.1	—	—	—
MANOVA result					
Wilks' λ , 7 df	1.6	2.4	—	—	—
<i>n</i>	33	31	—	—	—
Analysis 3					
Variable					
Concealment	3.5	3.0	2.8	-3.2	-0.3
Distance to water	0.9	-0.3	1.4	0.6	-0.9
MANOVA result					
Wilks' λ , 3 df	2.4	1.8	2.2	1.7	0.5
<i>n</i>	75	58	40	21	27

Note: Except where noted, *F* values shown are from ANOVAs controlling for relative nest-initiation date. A negative *F* value indicates a negative correlation with body mass. There were insufficient data to run any analysis for northern pintails, or to run analysis 2 on northern shovelers, American wigeon, or gadwall.

* $P < 0.05$.

ceived less insolation (also see Geiger 1959, pp. 279–281; Archibold et al. 1996). Since insolation contributes significantly to animals' thermal budgets (Robinson et al. 1976; DeJong 1979; Walsberg 1992, 1993), the overall conclusion is that greater thermal benefits accrue to smaller species' nest sites than to those of larger species, and this probably significantly reduces smaller species' metabolic costs. Our assumption was that larger species may not take advantage of these thermal benefits because of trade-offs with predation (Marzluff 1988; see below).

Our second finding was that smaller species nested later in the year, in both our own and other study areas. Larger waterfowl are able to make greater use of endogenous reserves during incubation because they have a greater capacity to store nutrients (Afton 1980; Afton and Paulus 1992) and use energy more efficiently than do smaller species (Schmidt-Nielsen 1984). Collectively, these constraints may prevent smaller species from nesting early in the year, when lower temperatures prevail (Bluhm 1992). Another consequence of the constraints may be that smaller species are prevented from reaching the breeding grounds as early as larger species; arrival times roughly correlate with initiation dates (Higgins et al. 1992; Petrula 1994). Relationships be-

tween nest-initiation date and ambient temperature are frequently reported (Smith 1971; Hammond and Johnson 1984; Higgins et al. 1992), but the influence of body mass on nest-initiation date has not previously been tested.

A third finding was that smaller species nested closer to wetlands. This correlation could be spurious if, for example, appropriate nest habitat for large species happened to be farther from water. However, based on measurements at 720 random non-nest sites on our study area (R.G. Clark, unpublished data), there is no significant relationship between distance to water and either concealment ($r = -0.0002$, $P = 0.99$) or vegetation height ($r = -0.03$, $P = 0.27$). The importance of proximity to wetlands is highlighted by some additional data. Average distances to water from nests on our study area were approximately 55, 108, and 119 m for blue-winged teal, mallard, and random non-nest sites, respectively. Blue-winged teal and mallards take, on average, three and one nest recess(es) per day over 24 and 28 days of incubation, respectively (Gloutney and Clark 1999). Therefore, on our study area, over the entire incubation period, blue-winged teal travelled, on average, a total of only 8.0 km from their actual nest sites, whereas they would have travelled 17.2 km from random sites. Equivalent total travel dis-

Table 3. Literature sources used to test for a relationship between nest-initiation date and body mass (see Fig. 3).

Species	Measure of central tendency extracted from paper	Source
Mallard, blue-winged teal, northern shoveler, American wigeon, gadwall, northern pintail, redhead (<i>Aythya americana</i>), lesser scaup (<i>A. affinis</i>)	Mean of 5 annual means (3 for mallard and redhead)	Keith 1961
Mallard, blue-winged teal, northern pintail, canvasback (<i>Aythya valisineria</i>)	Midpoint of average range	Stoudt 1971
Mallard, northern shoveler, northern pintail, green-winged teal (<i>Anas crecca</i>), Eurasian wigeon (<i>A. penelope</i>), greater scaup (<i>Aythya marila</i>), tufted duck (<i>A. fuligula</i>), common merganser (<i>Mergus merganser</i>), red-breasted merganser (<i>M. serrator</i>), white-winged scoter (<i>Melanitta fusca</i>)	Midpoint of average range	Väisänen 1974
Mallard, blue-winged teal, gadwall	Mean	Livezey 1981b
Mallard, blue-winged teal, gadwall, redhead	Mean	Hammond and Johnson 1984
Mallard, blue-winged teal, northern shoveler, gadwall, American wigeon, northern pintail, green-winged teal, lesser scaup	Midpoint of range of 99% of nest initiations	Higgins et al. 1992
Mallard, blue-winged teal, northern shoveler, gadwall, northern pintail	Median	Greenwood et al. 1995
Mallard, northern shoveler, American wigeon, northern pintail, green-winged teal, lesser scaup	Midpoint of range of 99% of nest initiations	Petrula 1994

tances for mallards are 6.0 and 6.6 km. Clearly, blue-winged teal saved much more energy than did mallards during a nutritionally stressful period. The trade-off with nesting close to water is that it could concentrate nests and increase profitability for, and attraction of, predators (cf. Lima 1985). For example, the area in which predators would have to search around circular wetlands with a radius of 50 m would be about 2.7 and 7.1 ha for teal and mallards, respectively. If these differences between species had important effects on predation rates, they could select for smaller species to nest closer to larger wetlands or to nest farther from wetlands.

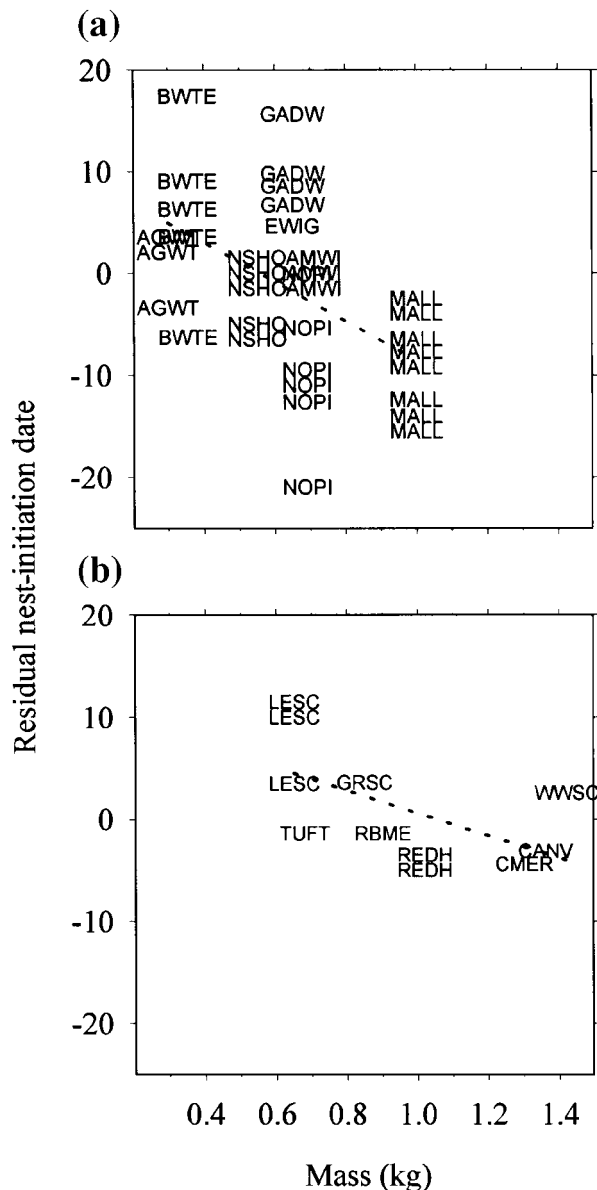
Because we predicted that smaller species would use less nest concealment, we also predicted that they would incur higher predation rates. However, despite support for the first prediction, we did not find that interspecific differences in body mass were associated with interspecific differences in nest-predation rate. This is consistent with the finding that, intraspecifically, neither concealment nor vegetation height is a significant discriminator of successful versus unsuccessful duck nests in our study area (Clark and Shutler 1999). A related finding is that early-nesting (i.e., larger) species typically suffer higher predation rates than late nesters (Beauchamp et al. 1996), which is a trend counter to our prediction (one way in which early nesters compensate for a higher predation rate is to renest more frequently; Sowl 1949, 1955). In addition, although benefits of concealment against predators are often reported (about 80% of the studies reviewed in Martin 1992), dense vegetation at nests may decrease the capacity of incubating females to detect or escape approaching predators (Götmark et al. 1995; Wiebe and Martin 1998). Hence, a variety of factors may make the trade-off between concealment and nest success more complex. In contrast to the pattern reported here for ducks, Marzluff (1988) found a trade-off between reduced nest concealment and increased nest predation on pinyon jays (*Gymnorhinus cyanocephalus*). He also found that pinyon

jays re-nested in less concealed sites if their nests failed because of low temperatures. It is not immediately clear which ecological differences between ducks and jays would be responsible for the different results.

Interspecific differences in plumage colour and density (Calder and King 1974), size and colour of unfeathered areas (Burt 1986), degree of nest insulation (Collias and Collias 1984), duration of embryonic development, efficiency of heat transfer to eggs (Calder and King 1974), or behavioural heat storage or loss (Calder and King 1974) could also influence the relationships observed here. The fact that our results were significant without the preceding factors being controlled for suggests that we have identified a key variable, namely body mass. Aside from its relationship to energetics, body mass is associated with a suite of life-history phenomena that influence other nesting behaviours (Collias and Collias 1984) and reproductive strategies (Sæther 1987; Afton and Paulus 1992; Alisauskas and Ankney 1992). For example, smaller duck species have shorter life-spans than larger species, and they are more reluctant to flush from their nests, probably because of the relatively greater value of their nests (Forbes et al. 1994). However, although suites of strategies can evolve in concert, they need not do so (Shutler and Weatherhead 1990). For example, Lapland longspurs (*Calcarius lapponicus*) and snow buntings (*Plectrophenax nivalis*) have radically different nesting behaviours despite their close phylogenetic affinity. Lapland longspurs nest in the open, and incubating females are seldom fed by their mates, whereas snow buntings nest underground in cooler sites that require continuous incubation and frequent feeding of the female by the male (Lyon and Montgomerie 1987). Such radical differences in nesting ecology do not occur among the waterfowl species in the present study.

In contrast to significant interspecific results, we found no compelling evidence for intraspecific relationships between

Fig. 3. Residual nest-initiation date (after publication source and foraging niche were controlled for) relative to female body mass for dabblers (a) and non-dabblers (b) (see the text; for data sources see Table 3). AGWT, green-winged teal; BWTE, blue-winged teal; NSHO, northern shoveler; GADW, gadwall; EWIG, Eurasian wigeon; NOPI, northern pintail; AMWI, American wigeon; MALL, mallard; LESC, lesser scaup; TUFT, tufted duck; GRSC, greater scaup; RBME, red-breasted merganser; REDH, redhead; CMER, common merganser; CANV, canvasback; WWSC, white-winged scoter. Dotted lines show regressions.



body mass and nest-site concealment, distance to water, or duration. There are several possible reasons for this. First, some variation in metabolism is independent of body mass, and this could obscure intraspecific relationships with nesting ecology, especially since intraspecific variation in body mass is much less than interspecific variation. Second, body mass within a species may be an inappropriate metric of surface area, and hence of energetic constraints. Third, our

sample sizes may have been too small to allow these effects to be detected. Similarly, a number of studies have failed to show a relationship between intraspecific variation in avian body mass and energy expenditure, even during times of energetic stress (e.g., nestling care; reviewed in Tinbergen and Dietz 1994). There may be numerous trade-offs that obscure the latter relationship, such as locomotory costs associated with carrying extra mass (Tinbergen and Dietz 1994). We were unable to test intraspecifically whether nest-initiation date was influenced by body mass because the species that we study frequently reneest. In the Arctic, geese have less opportunity for reneesting, and the data here are conflicting; Cooch et al. (1992) found that body size of lesser snow geese (*Chen caerulescens*) had no influence on laying date, whereas Bon (1997) found that larger Ross' geese (*Anser rossii*) nested earlier.

Thermal consequences of nest-site choice have frequently been identified (e.g., Ricklefs and Hainsworth 1969; Austin 1974; Seddon and Davis 1989; Clark et al. 1990; Facemire et al. 1990; With and Webb 1993; Gloutney and Clark 1997; Stokes and Boersma 1998), but their connections to body mass and energetic constraints have seldom been tested or clearly enunciated. Similar statements could be made about relationships between body mass and nest-initiation date, and between body mass and proximity to food (in this study, distance to water). We found strong evidence that body mass affects each of these aspects of waterfowl nesting ecology. We propose that these differences are metabolically driven. A larger sample of species would provide a stronger test of this hypothesis, and provide the opportunity to evaluate the effects of phylogeny on this relationship (Harvey and Pagel 1991; for a phylogeny of *Anas* see Livezey 1991).

Acknowledgements

This paper would not have happened had there not been dedicated fieldwork from more than 50 people, to whom we express sincere gratitude. Funding was provided by grants to R.G. Clark from the Canadian Wildlife Service and the Natural Sciences and Engineering Research Council of Canada. Ray Alisauskas, Adele Mullie, and Stuart Slattery suggested some useful references. We thank two anonymous reviewers for comments, James Sedinger for prompt assistance, and Mark Petrula for providing a copy of his thesis.

References

- Afton, A. 1980. Factors affecting incubation rhythms of Northern Shovelers. *Condor*, **82**: 132–137.
- Afton, A.D., and Paulus, S.L. 1992. Incubation and brood care. In *Ecology and management of breeding waterfowl*. Edited by B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu. University of Minnesota Press, Minneapolis. pp. 62–108.
- Alisauskas, R.T., and Ankney, C.D. 1992. The cost of egg laying and its relationship to nutrient reserves in waterfowl. In *Ecology and management of breeding waterfowl*. Edited by B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu. University of Minnesota Press, Minneapolis. pp. 30–61.

- Alisauskas, R.T., and Ankney, C.D. 1994. Nutrition of breeding Ruddy Ducks: the role of nutrient reserves. *Condor*, **96**: 878–897.
- Ankney, C.D., and Alisauskas, R.T. 1991. The use of nutrient reserves by breeding waterfowl. *Proc. Int. Ornithol. Congr.* **20**: 2170–2176.
- Archibold, O.W., Ripley, E.A., and Bretell, D.L. 1996. Comparison of the microclimates of a small aspen grove and adjacent prairie in Saskatchewan. *Am. Midl. Nat.* **136**: 248–261.
- Austin, G.T. 1974. Nesting success of the Cactus Wren in relation to nest orientation. *Condor*, **76**: 216–217.
- Beauchamp, W.D., Koford, R.R., Nudds, T.D., Clark, R.G., and Johnson, D.H. 1996. Long-term declines in nest success of prairie ducks. *J. Wildl. Manage.* **60**: 247–257.
- Blem, C.R. 1990. Avian energy storage. *In Current ornithology 7. Edited by D.M. Power.* Plenum Press, New York. pp. 59–113.
- Bluhm, C.K. 1992. Environmental and endocrine control of waterfowl reproduction. *In Ecology and management of breeding waterfowl. Edited by B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu.* University of Minnesota Press, Minneapolis. pp. 323–364.
- Bon, R.L. 1997. Spring nutritional ecology of migrating and breeding Ross' geese *Anser rosii*. M.Sc. Thesis, University of Saskatchewan, Saskatoon.
- Burger, J. 1972. The use of a fish-eye lens to study nest placement in Franklin's Gulls. *Ecology*, **53**: 562–564.
- Burt, E.H., Jr. 1986. An analysis of the physical, physiological, and optical aspects of avian coloration with emphasis on Wood-warblers. *Ornithol. Monogr.* No. 38.
- Calder, W.A., and King, J.R. 1974. Thermal and caloric relations of birds. *In Avian biology IV. Edited by D.S. Farner and J.R. King.* Academic Press, New York. pp. 259–413.
- Charnov, E.L. 1976. Optimal foraging: the marginal value theorem. *Theor. Popul. Biol.* **9**: 129–136.
- Clark, L., Schreiber, R.W., and Schreiber, E.A. 1990. Pre- and post-El Niño southern oscillation comparison of nest sites for Red-tailed Tropicbirds breeding in the central Pacific Ocean. *Condor*, **92**: 886–896.
- Clark, R.G., and Shutler, D. 1999. Avian habitat selection: adaptive nest-site choice by ducks. *Ecology*, **80**. In press.
- Collias, N.E., and Collias, E.C. 1984. Nest building and bird behavior. Princeton University Press, Princeton, N.J.
- Cooch, E.G., Lank, D.B., Rockwell, R.F., and Cooke, F. 1992. Is there a positive relationship between body size and fecundity in Lesser Snow Geese? *Auk*, **109**: 667–673.
- DeJong, A.A. 1979. Thermal irradiation preferences of white-crowned sparrows in relation to ambient temperature. *Physiol. Behav.* **22**: 157–171.
- Duncan, D.C. 1987a. Variation and heritability in egg size of the northern pintail. *Can. J. Zool.* **65**: 992–996.
- Duncan, D.C. 1987b. Nest site distribution and overland brood movements of northern pintails in Alberta. *J. Wildl. Manage.* **51**: 716–723.
- Facemire, C.F., Facemire, M.F., and Facemire, M.C. 1990. Wind as a factor in the orientation of entrances of Cactus Wren nests. *Condor*, **92**: 1073–1075.
- Forbes, M.R.L., Clark, R.G., Weatherhead, P.J., and Armstrong, T. 1994. Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. *Behav. Ecol. Sociobiol.* **34**: 79–85.
- Geiger, R. 1959. The climate near the ground. Harvard University Press, Cambridge, Mass.
- Gloutney, M.L. 1996. Nest-site selection, energetics of reproduction and comparative behaviour of mallard (*Anas platyrhynchos*) and blue-winged teal (*Anas discors*). Ph.D. thesis, University of Saskatchewan, Saskatoon.
- Gloutney, M.L., and Clark, R.G. 1997. Nest-site selection by Mallard and Blue-winged Teal in relation to microclimate. *Auk*, **114**: 381–395.
- Gloutney, M.L., and Clark, R.G. 1999. Clutch size and incubation periods in Mallard and Blue-winged Teal. *Wilson Bull.* **111**. In press.
- Gloutney, M.L., Clark, R.G., Afton, A.D., and Huff, G.J. 1993. Timing of nest searches for upland nesting waterfowl. *J. Wildl. Manage.* **57**: 597–601.
- Gloutney, M.L., West, N.G., and Clark, R.G. 1996. Metabolic costs of incubation and clutch size determination in the red junglefowl, *Gallus gallus spadiceus*. *Comp. Biochem. Physiol. A*, **114**: 265–270.
- Götmark, F., Blomqvist, D., Johansson, O.C., and Bergkvist, J. 1995. Nest site selection: a tradeoff between concealment and view of the surroundings? *J. Avian Biol.* **26**: 305–312.
- Greenwood, R.J., Sargeant, A.G., Johnson, D.H., Cowardin, L.M., and Shaffer, T.L. 1995. Factors associated with duck nest success in the Prairie Pothole Region of Canada. *Wildl. Monogr.* No. 128.
- Hammond, M.C., and Johnson, D.H. 1984. Effects of weather on breeding ducks in North Dakota. U.S. Fish Wildl. Tech. Rep. No. 1.
- Harvey, P.H., and Pagel, M.D. 1991. The comparative method in evolutionary biology. Oxford University Press, New York.
- Higgins, K.F., Kirsch, L.M., Klett, A.T., and Miller, H.W. 1992. Waterfowl production on the Woodworth Station in south-central North Dakota. U.S. Fish Wildl. Serv. Resour. Publ. No. 180.
- Hochbaum, H.A. 1944. The canvasback on a prairie marsh. 3rd ed. American Wildlife Institute, Washington, D.C.
- Hogan, J.A. 1989. The interaction of incubation and feeding in broody junglefowl hens. *Anim. Behav.* **38**: 121–128.
- Johnson, D.H. 1979. Estimating nest success: the Mayfield method and an alternative. *Auk*, **96**: 651–661.
- Keith, L.B. 1961. A study of waterfowl ecology on small impoundments in southeastern Alberta. *Wildl. Monogr.* No. 6.
- Klett, A.T., Duebbert, H.F., Faanes, C.A., and Higgins, K.F. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish Wildl. Serv. Resour. Publ. No. 158.
- Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
- Lima, S.L. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a tradeoff in the black-capped chickadee. *Oecologia*, **66**: 60–67.
- Livezey, B.C. 1981a. Locations and success of duck nests evaluated through discriminant analysis. *Wildfowl*, **32**: 23–27.
- Livezey, B.C. 1981b. Duck nesting in retired croplands of Horicon National Wildlife Refuge, Wisconsin. *J. Wildl. Manage.* **45**: 27–37.
- Livezey, B.C. 1991. A phylogenetic analysis and classification of recent dabbling ducks (tribe Anatini) based on comparative morphology. *Auk*, **108**: 471–507.
- Lyon, B.E., and Montgomerie, R.D. 1987. Ecological correlates of incubation feeding: a comparative study of high arctic finches. *Ecology*, **68**: 713–722.
- Martin, T.E. 1988. On the advantage of being different: nest predation and the coexistence of bird species. *Ecology*, **85**: 2196–2199.
- Martin, T.E. 1992. Breeding productivity considerations: what are the appropriate habitat features for management? *In Ecology*

- and conservation of Neotropical migrant landbirds. *Edited by J.M. Hagan III and D.W. Johnston*. Smithsonian Institution Press, Washington, D.C. pp. 455–473.
- Martin, T.E. 1996. Fitness costs of resource overlap among coexisting birds species. *Nature (Lond.)*, **380**: 338–340.
- Marzluff, J.M. 1988. Do pinyon jays alter nest placement based on prior experience? *Anim. Behav.* **36**: 1–10.
- McArthur, A.J. 1990. Thermal interaction between animal and microclimate: specification of a “standard environmental temperature” for animals outdoors. *J. Theor. Biol.* **148**: 331–343.
- Montgomerie, R.D., and Weatherhead, P.J. 1988. Risks and rewards of nest defence by parent birds. *Q. Rev. Biol.* **63**: 167–187.
- Murton, R.K., and Westwood, N.J. 1977. *Avian breeding cycles*. Clarendon Press, Oxford.
- Peters, R.H. 1983. *The ecological implications of body size*. Cambridge University Press, Cambridge.
- Petrula, M.J. 1994. Nesting ecology of ducks in interior Alaska. M.S. thesis, University of Alaska, Fairbanks.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.
- Ricklefs, R.E. 1969. An analysis of nestling mortality in birds. *Smithson. Contrib. Zool.* No. 9.
- Ricklefs, R.E., and Hainsworth, F.R. 1969. Temperature regulation in nestling Cactus Wrens: the nest environment. *Condor*, **71**: 32–37.
- Robinson, D.E., Campbell, G.S., and King, J.R. 1976. An evaluation of heat exchange in small birds. *J. Comp. Physiol.* **105**: 153–166.
- Rohwer, F.C. 1992. The evolution of reproductive patterns in waterfowl. *In Ecology and management of breeding waterfowl. Edited by B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec, and G.L. Krapu*. University of Minnesota Press, Minneapolis. pp. 486–539.
- Sæther, B.E. 1987. The influence of body weight on the covariation between reproductive traits in European birds. *Oikos*, **48**: 79–88.
- SAS Institute, Inc. 1989. *SAS language and procedures: usage*. Version 6. 1st ed. SAS Institute Inc., Cary, N.C.
- Schmidt-Nielsen, K. 1984. *Scaling: Why is animal size so important?* Cambridge University Press, Cambridge.
- Seddon, P.J., and Davis, L.S. 1989. Nest-site selection by Yellow-eyed Penguins. *Condor*, **91**: 653–659.
- Shutler, D., and Weatherhead, P.J. 1990. Targets of sexual selection: song and plumage of wood warblers. *Evolution*, **44**: 1967–1977.
- Smith, A.G. 1971. Ecological factors affecting waterfowl production in the Alberta Parklands. U.S. Fish Wildl. Serv. Resour. Publ. No. 98.
- Sorci, G., Clobert, J., and Michalakis, Y. 1996. Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. *Oikos*, **76**: 121–130.
- Sowls, L.K. 1949. A preliminary report on reneesting in waterfowl. *Trans. N. Am. Wildl. Conf.* **14**: 260–273.
- Sowls, L.K. 1955. *Prairie ducks*. University of Nebraska Press, Lincoln.
- Stokes D.L., and Boersma, P.D. 1998. Nest-site characteristics and reproductive success in Magellanic Penguins (*Spheniscus magellanicus*). *Auk*, **115**: 34–49.
- Stoudt, J.H. 1971. Ecological factors affecting waterfowl production in the Saskatchewan parklands. U.S. Fish Wildl. Serv. Resour. Publ. No. 99.
- Sugden, L.G., and Beyersbergen, G.W. 1985. Farming intensity on waterfowl breeding grounds in Saskatchewan parklands. *Wildl. Soc. Bull.* **12**: 22–26.
- Sugden, L.G., and Beyersbergen, G.W. 1986. Effect of density and concealment on American crow predation of simulated duck nests. *J. Wildl. Manage.* **50**: 9–14.
- Tinbergen, J.M., and Dietz, M.W. 1994. Parental energy expenditure during brood rearing in the Great Tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* **8**: 563–572.
- Väisänen, R.A. 1974. Timing of waterfowl breeding on the Krunnit Islands, Gulf of Bothnia. *Ornis Fenn.* **51**: 61–84.
- Walsberg, G.E. 1981. Nest-site selection and the radiative environment of the Warbling Vireo. *Condor*, **83**: 86–88.
- Walsberg, G.E. 1985. Physiological consequences of microhabitat selection. *In Habitat selection in birds. Edited by M.L. Cody*. Academic Press, Toronto. pp. 389–413.
- Walsberg, G.E. 1992. Quantifying radiative heat gain in animals. *Am. Zool.* **32**: 217–224.
- Walsberg, G.E. 1993. Thermal consequences of diurnal microhabitat selection in a small bird. *Ornis Scand.* **24**: 217–224.
- Weller, M.W. 1956. A simple field candler for waterfowl eggs. *J. Wildl. Manage.* **20**: 111–113.
- Wiebe, K.L., and Martin, K. 1998. Costs and benefits of nest cover for ptarmigan: changes within and among years. *Anim. Behav.* **56**: 1137–1144.
- With, K.A., and Webb, D.R. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. *Condor*, **95**: 401–413.
- Wolf, B.O., and Walsberg, G.E. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology*, **77**: 2228–2236.