Factors influencing investigator-caused nest abandonment by North American dabbling ducks

P.R. Garrettson, K.D. Richkus, F.C. Rohwer, and W.P. Johnson

Abstract: We examined factors (species, nest age, nest initiation date, clutch size, predator activity) that may affect the probability of investigator-caused nest abandonment in North American dabbling ducks and made predictions based on parental investment theory. For all nests, the best model contained species, nest stage, nest initiation date, and the interaction of species with nest initiation date. The probability of abandonment by Mallards (Anas platyrhynchos L., 1758) was consistently higher than that of Blue-winged Teal (Anas discors L., 1766). In these species, abandonment probability increased with later date, whereas Gadwall (Anas strepera L., 1758), Northern Pintails (Anas acuta L., 1758), and Northern Shovelers (Anas clypeata L., 1758) showed the opposite pattern. Abandonment by all species declined as nest stage increased. Early-laying (<5 eggs) females were 7 times more likely, and late-laying females were twice as likely, to abandon nests as incubating females. During incubation, abandonment probability was 38% higher during early (<8 days) incubation than late incubation, and for each additional egg in a completed clutch, it was 19% lower. We propose a novel, two-stage model in which dabbling duck nest abandonment is influenced predominantly by opportunities for future reproduction during laying, and expected benefits from the current reproductive event during incubation.

Résumé : Nous examinons les facteurs (espèce, âge du nid, date du début de construction du nid, taille de la couvée, activité des prédateurs) qui peuvent affecter la probabilité de l’abandon du nid à la suite d’une intervention d’un chercheur chez des canards barboteurs nord-américains et nous faisons des prédicitions basées sur la théorie de l’investissement parental. Pour l’ensemble des nids, le meilleur modèle contient l’espèce, le stade du nid, la date du début de construction du nid et l’interaction entre l’espèce et la date de début de construction du nid. La probabilité d’abandon chez les canards colverts (Anas platyrhynchos L., 1758) est constamment plus élevée que chez les sarcelles à ailes bleues (Anas discors L., 1766). Chez ces espèces, la probabilité d’abandon augmente en fonction des dates plus tardives, alors que le patron contraire s’observe chez les canards chipeaux (Anas strepera L., 1758), les canards pilets (Anas acuta L., 1758) et les canards souchets (Anas clypeata L., 1758). L’abandon par toutes les espèces diminue à mesure que le stade du nid progresse. Les pondeuses hâtives (≤5 œufs) sont 7 fois et les pondeuses tardives 2 fois plus susceptibles d’abandonner leur nid que les femelles couveuses. Durant l’incubation, la probabilité d’abandon est 38 % plus élevée au début de la période (≤8 jours) qu’à la fin; elle diminue de 19 % pour chaque œuf additionnel dans la couvée totale. Nous proposons un modèle nouveau en deux étapes dans lequel l’abandon du nid par les canards barboteurs est influencé surtout par les occasions de reproduction future durant la ponte et les bénéfices attendus par l’épisode actuel de reproduction durant l’incubation.

Introduction

Nest abandonment caused by investigators is an unfortunate byproduct of research on nesting ducks, but studying it can provide insight into the ecology and evolution of parental investment. We tested two hypotheses about nest abandonment: (1) abandonment of the current nest should decrease as females’ chances for future reproductive events decrease; (2) abandonment should be inversely related to expected benefits from the current reproductive attempt (from Ackerman and Eadie 2003). We examined investigator-induced abandonment using nests of five species of ducks: Mallards (Anas platyrhynchos L., 1758), Gadwall (Anas strepera L., 1758), Blue-winged Teal (Anas discors L., 1766), Northern Shovelers (Anas clypeata L., 1758), and Northern Pintails (Anas acuta L., 1758). We assessed the influence of species, nest age, nest initiation date, clutch size, and predation risk (indexed by year–site specific nest success) on the probability of abandonment.

The future reproduction hypothesis predicts that species
with greater opportunities for future reproduction, either by renesting in the current year or by reproduction in subsequent years, would have higher nest abandonment probabilities. Therefore, we predicted that species that are larger bodied (which is correlated with longevity and annual survival, especially within tribes; Krementz et al. 1997), and have a strong propensity for renesting, would exhibit the highest abandonment probabilities (Table 1). We chose body mass rather than longevity, which can be biased by the number of band recoveries (Arnold 1988) or survival probability based on band recovery data (Krementz et al. 1989), because we lacked comparable estimates for all species. Based on our ranking, we predicted that Mallards would exhibit the highest probability of nest abandonment, followed by Northern Pintails, Gadwall, Northern Shovelers, and Blue-winged Teal.

The future reproduction hypothesis and the expected benefits hypothesis both predict that nest abandonment should decrease with nest age, but they predict different patterns of decline. Ducks typically only renest after the loss of a nest, and the probability of renesting declines with increasing age of the failed nest (Sowls 1955; Strohmeyer 1967), though likely not at a constant rate. Renesting propensity is higher (Arnold et al. 2010) and renest interval is shorter (Richkus 2002; Arnold et al. 2010) during laying than during incubation. Therefore, the potential for future reproduction hypothesis predicts an abrupt decrease in abandonment probability when incubation begins (Forbes et al. 1994). Alternatively, older nests offer greater expected benefits to the female simply because they are closer to hatch than younger nests and must survive fewer days of exposure to predators (Mayfield 1961, 1975) and other hazards (Krapu 2000) before hatch. These benefits accrue at a slightly increasing (Mayfield 1961, 1975) rate from nest initiation to hatch, so the expected benefits hypothesis predicts a steady decrease in abandonment probability with increasing nest age.

Predictions from the expected benefits hypothesis concerning abandonment relative to nest initiation date conflict with predictions from the future reproduction hypothesis. Later-season nests provide fewer expected benefits to females (Weatherhead 1989) because brood survival (Orthmeyer and Ball 1990; Rotella and Ratti 1992; Dzus and Clark 1998; Krapu et al. 2000) and postfledgling survival (reviewed in Rohwer 1998) decline with later date. Thus, the expected benefits hypothesis predicts abandonment to increase with nest initiation date. However, the future reproduction hypothesis predicts reduced abandonment with later nest initiation because a female that initiates a nest later in the season has a lower probability of renesting if she loses or abandons that nest (Richkus 2002; Arnold et al. 2010). This prediction of the future reproduction hypothesis is complicated by the integration of within season and lifetime reproductive events. Females that abandon a late-season nest have little chance of renesting, but they may improve their probability of surviving to the subsequent nesting season by avoiding a delayed molt and fall migration. A finding of reduced abandonment later in the season supports the renesting (within season) component of the future reproduction hypothesis. In contrast, a finding of more abandonment later in the season supports the next breeding season component of the future reproduction hypothesis and it also supports the expected benefits hypothesis.

The future reproduction hypothesis predicts that females that perceive a higher risk of predation would be more likely to abandon nests. If females can assess the presence of predators, and if predation risk is a factor in abandonment, then higher abandonment probabilities on sites with more predator activity would preserve their opportunities for future reproduction via increased survival. The risk to a nesting dabbling duck female is serious, as red foxes (Vulpes vulpes (L., 1758)) kill more than 900 000 nesting female Mallards (Sargeant et al. 1984) annually in North America.

We predicted, based on the expected benefits hypothesis, that females with large clutches would be less likely to abandon nests compared with females with smaller clutches at the same date. The larger the clutch, the greater the expected benefit of the current reproductive attempt to the female (Rohwer 1985; Lessells 1986; Montgomerie and Weatherhead 1988; Lepage et al. 1998; Mallory et al. 1998). If the nest hatches, a relatively large clutch provides a greater reproductive payoff than a small clutch, and because waterfowl have precocial young, there is little or no cost to rearing an extra duckling (Rohwer 1985; Lessells 1986).

Numerous studies, many in passerines, have examined the intensity of offspring defense (e.g., aggressive behavior, distraction displays) to test hypotheses about parental investment relative to risk-taking behavior (reviewed in Montgomerie and Weatherhead 1988). In waterfowl, some studies have focused on flushing distance, which is an analogous expression of parental care and risk-taking behavior (Forbes et al. 1994; Mallory et al. 1998; Gunness et al. 2001; Gunnness and Weatherhead 2002). However, studying offspring desertion (reviewed in Szekely et al. 1996) rather than mere defense provides clearer tests of parental investment hypotheses, as parents can still benefit from lightly defended young (Ackerman and Eadie 2003), whereas there is no benefit to a female duck from an abandoned nest (Armstrong and Robertson 1988).

In waterfowl, much work has focused on clutch size manipulations of incubation-stage nests (Armstrong and Robertson 1988; Ackerman and Eadie 2003; Ackerman et al. 2003) and found that abandonment decreased with a higher proportion of the clutch remaining and with incubation stage, consistent with the expected benefits hypothesis. Moreover, by experimentally equalizing expected benefits from the clutch, Ackerman and Eadie (2003) persuasively argued that the observed patterns were due to expected benefits, not the influence of past investment on future reproduction. However, Forbes et al. (1994) included laying-stage nests and found species differences consistent with the future reproduction hypothesis, but only during laying. They also found higher abandonment of laying-stage than incubation-stage nests.

The theoretical groundwork and use of experimentation in prior waterfowl studies is impressive, but many earlier studies were limited to incubation-stage nests, covered few species, or had small sample sizes. Our large data set allowed us to examine nests of several species throughout the nesting cycle, as well as to test for the potential effects of nest initiation date and nest depredation rate. We synthesized our
### Table 1. Renesting potential and body mass of five North American dabbling duck species.

<table>
<thead>
<tr>
<th>Species (Genus)</th>
<th>Percent renesting (following loss of first nest)</th>
<th>Mean no. of nests/female</th>
<th>Body mass (g)</th>
<th>Relative ranking (1, greatest potential for future reproduction)</th>
<th>References</th>
</tr>
</thead>
</table>
| **Mallard** (*Anas platyrhynchos*) | 100 85 | Color-marked 2.2 Anchor-and-suture radio transmitters 1.4–2.0 | 1098 | 1 | Keith 1961  
Richkus 2002;  
Paquette et al. 1997 |
| **Northern Pintail** (*Anas acuta*) | 30 61–90 56 55–85 | Color-marked na Anchor-and-suture radio transmitters | 860 | 2 | Sowls (1955)  
Richkus 2002  
Grand and Flint 1996  
Guyn and Clark 2000 |
| **Gadwall** (*Anas strepera*) | 82 74 | Color-marked 1.6 | 828 | 3 | Keith 1961  
Gates 1962  
Sowls 1949; Keith 1961 |
| **Northern Shoveler** (*Anas clypeata*) | 21 75 | Color-marked 1.4 | 634 | 4 | Keith 1961  
Sowls 1949; Keith 1961 |
| **Blue-winged Teal** (*Anas discors*) | 33 55 | Color-marked; backpack-harness transmitters 1.3 | 374 | 5 | Strohmeyer 1967;  
Rohwer 1986; Keith 1961  
Keith 1961 |

**Note:** Percent renesting and mean number of nests/female are likely underestimated to varying degrees depending on marking method, with the greatest underestimation in color-marked birds and the least with abdominally implanted radio transmitters (for details see references). Predictions of potential for future reproduction are based on the assumption that larger birds live longer and have higher annual survival (Krementz et al. 1989); body masses are mean values for adult females (Bellrose 1980).
results and prior work to propose a new model for understanding nest abandonment and parental investment in temperate-nesting ducks.

Materials and methods

Study sites and field protocol

We used data from two studies of dabbling duck nesting. One was conducted from 1994 to 1996 in north-central North Dakota (USA) on the effects of mammalian predator removal on dabbling duck nest success; this study encompassed 19 study sites (16 were 41.5 km² each, 3 were 2.6 km²), 11 of which were trapped from late March to early April (Garretson and Rohwer 2001; P.R. Garretson, unpublished data). The other, on nest site selection and renesting by Northern Pintails, took place on a single site (41.5 km²) in southern Saskatchewan (Canada) from 1998 to 2000 (Richkus 2002). Sites in both studies comprised a mixture of cropland, grassland, and wetlands. The large sites in North Dakota averaged 28% ± 7% (range 10%–69%) grass cover, whereas small sites averaged 58% ± 16% (range 50%–75%) grass cover; the site in Saskatchewan had 21% grass cover.

We found upland duck nests by dragging a chain between two tractors or all-terrain vehicles (Klett et al. 1986), or incidentally while walking to do other fieldwork. Clutch size and incubation stage were recorded (Weller 1956) on each nest visit. Nests were revisited every 7–14 days until a fate (abandoned, hatched, or destroyed) was determined. Nests for which a fate was not determined were excluded from analyses. We grouped all usable nests into two categories: (1) those abandoned after the first visit owing to investigator disturbance and (2) those the female continued to attend. We assumed nest abandonment was due to investigator disturbance if additional eggs had not been laid or if incubation had not progressed immediately following a nest visit. We only considered the nest fate immediately following the first visit (when we found it), so we avoided the potential effect of increased abandonment with multiple nest visits (Knight and Temple 1986; Gunnness and Weatherhead 2002). The vast majority of abandonment owing to investigator activity occurred immediately after the first visit. We categorized abandonment owing to other (e.g., weather) or unknown reasons (i.e., the female returned to nest following our initial nest visit, leaving evidence of her return in the form of additional eggs laid, progression of incubation, and (or) disturbance of nest material, but subsequently abandoned the nest prior to our second visit) in the continued attendance category.

Statistical analyses

We considered incubation-stage nests and all nests in two separate logistic regression (SAS Institute Inc. 1990; Stokes et al. 1995; Agresti 1996) analyses because of two factors. First, we predicted that the probability of abandonment would be different for laying-stage and incubation-stage nests, owing to the sharp drop in the capacity for renesting with the onset of incubation, and the increase in renesting interval that occurs once females begin incubating (Sowls 1949, 1955; Gates 1962; Strohmeyer 1967; Arnold et al. 2010). Secondly, we were interested in the effects of clutch size, and final clutch size cannot be determined until incubation has begun. In both cases, we used information–theoretic methods (Burnham and Anderson 1998, 2002) to assess the influence of species (Mallard, Gadwall, Blue-winged Teal, Northern Pintail, and Northern Shoveler), nest age when found (treated as a categorical variable), nest initiation date (treated as a continuous variable), and the nest success estimate (Garretson and Rohwer 2001; Richkus 2002) for the year–site combination, which was also treated as a continuous variable. We used nest success (Mayfield 1961, 1975) as a surrogate for predation activity, as >90% of nest failures were due to predators (Garretson 1999; Richkus 2002). Candidate models (Tables 2, 3) contained various combinations of these variables and reflected our predictions about factors affecting nest desertion. In the analysis of all nests, nest age was divided into three categories (≤5 eggs laid, ≥6 eggs laid, and all incubation-stage nests), because we suspected that abandonment probability might differ between nests found during early and late laying.

In a separate analysis of incubation-stage nests only, we divided the incubation period into two categories (≤8 days incubation, and ≥9 days of incubation). This cutoff was based on our experience with nesting ducks and also followed Ackerman and Eadie (2003). We also included clutch size, as well as all predictor variables from the analysis of all nests in our set of candidate models. In ducks, clutch size typically declines seasonally (reviewed in Rohwer 1992), so we wanted to obtain a measure of the relative investment in clutches by females of the same species, at the same point during the nesting season. Therefore, we regressed clutch size against nest initiation date for each species separately. The size and sign of the residuals from this regression correspond to the relative investment in the clutch (Rohwer 1988), and we used these date- and species-adjusted clutch values in appropriate candidate models (Table 3) to test for the effects of clutch size on abandonment probability.

In all cases, we chose among models based on second-order AIC differences adjusted for small sample size (ΔAICc) and Akaike weights (wi) (Burnham and Anderson 1998). We reported predicted abandonment probabilities and 95% confidence intervals based on the best model or averaged models (Tables 2, 3). Where appropriate we reported odds, odds ratios, and their 95% confidence intervals (Agresti 1996) to illustrate the magnitude and source of difference among predictor variables.

Results

Of the 5230 nests found, 4600 were suitable for and used in our analyses; 3007 were from the study in North Dakota and 1593 were from the study in Saskatchewan. Blue-winged Teal (n = 1823) were the most common, followed by Mallards (n = 1208), Gadwall (n = 602), Northern Pintails (n = 593), and Northern Shovelers (n = 308). We also found nests of Green-winged Teal (Anas crecca L., 1758; n = 43) and American Wigeon (Anas americana Gmelin, 1789; n = 23) on our study sites.

In the analysis of all nests, the best model contained species, nest age, nest initiation date, and the interaction of nest initiation date and species (Table 2). This model alone
Table 2. Logistic regression models predicting abandoned \((n = 324)\) versus non-abandoned \((n = 4103)\) nests of dabbling ducks \((Anas\ spp.)\) using data collected in North Dakota (1994–1996) and Saskatchewan (1998–2000).

<table>
<thead>
<tr>
<th>All nests model</th>
<th>(K)</th>
<th>(\Delta AIC_c)</th>
<th>(w_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species, age, date, species (\times) date</td>
<td>12</td>
<td>0.00</td>
<td>0.9822</td>
</tr>
<tr>
<td>Species, age</td>
<td>7</td>
<td>9.24</td>
<td>0.0097</td>
</tr>
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<td>Species, age, date</td>
<td>8</td>
<td>10.69</td>
<td>0.0047</td>
</tr>
<tr>
<td>Species, age, nesuc</td>
<td>8</td>
<td>11.44</td>
<td>0.0032</td>
</tr>
<tr>
<td>Species, age, species (\times) age</td>
<td>15</td>
<td>17.86</td>
<td>0.0001</td>
</tr>
<tr>
<td>Species, age, date, species (\times) age</td>
<td>16</td>
<td>19.69</td>
<td>(5 \times 10^{-5})</td>
</tr>
<tr>
<td>Age</td>
<td>3</td>
<td>22.40</td>
<td>(1 \times 10^{-5})</td>
</tr>
<tr>
<td>Age, date</td>
<td>4</td>
<td>24.43</td>
<td>(5 \times 10^{-6})</td>
</tr>
<tr>
<td>Age, date, age (\times) date</td>
<td>6</td>
<td>24.95</td>
<td>(4 \times 10^{-5})</td>
</tr>
<tr>
<td>Species, date</td>
<td>6</td>
<td>167.02</td>
<td>(5 \times 10^{-37})</td>
</tr>
<tr>
<td>Species, date, species (\times) date</td>
<td>10</td>
<td>168.09</td>
<td>(3 \times 10^{-37})</td>
</tr>
<tr>
<td>Species, nesuc, date, species (\times) date</td>
<td>11</td>
<td>169.16</td>
<td>(2 \times 10^{-37})</td>
</tr>
<tr>
<td>Species, nesuc, date</td>
<td>7</td>
<td>180.29</td>
<td>(7 \times 10^{-40})</td>
</tr>
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<td>Species, nesuc</td>
<td>6</td>
<td>185.32</td>
<td>(6 \times 10^{-41})</td>
</tr>
<tr>
<td>Species</td>
<td>5</td>
<td>185.58</td>
<td>(5 \times 10^{-41})</td>
</tr>
<tr>
<td>Species, nesuc, species (\times) nesuc</td>
<td>10</td>
<td>188.77</td>
<td>(1 \times 10^{-41})</td>
</tr>
<tr>
<td>Date</td>
<td>2</td>
<td>204.35</td>
<td>(4 \times 10^{-45})</td>
</tr>
<tr>
<td>Species, age, date, age (\times) date</td>
<td>10</td>
<td>274.13</td>
<td>(3 \times 10^{-60})</td>
</tr>
</tbody>
</table>

\(\Delta AIC_c\) of the top model was 2115.5.

Note: Number of parameters \((K)\), difference in Akaike’s information criterion adjusted for small sample size \((\Delta AIC_c)\), and Akaike weights \((w_i)\). Variables are species, age (early lay, late lay, incubation), date (julian date), nesuc (year–site specific nest success).


<table>
<thead>
<tr>
<th>Incubation-stage model</th>
<th>(K)</th>
<th>(\Delta AIC_c)</th>
<th>(w_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Incstage, rcsf</td>
<td>3</td>
<td>0.00</td>
<td>0.4573</td>
</tr>
<tr>
<td>Incstage, date, rcsf</td>
<td>4</td>
<td>1.91</td>
<td>0.1759</td>
</tr>
<tr>
<td>Rcsf</td>
<td>2</td>
<td>1.96</td>
<td>0.1717</td>
</tr>
<tr>
<td>Date, rcsf</td>
<td>3</td>
<td>3.96</td>
<td>0.0632</td>
</tr>
<tr>
<td>Incstage</td>
<td>2</td>
<td>4.30</td>
<td>0.0534</td>
</tr>
<tr>
<td>Species, incstage, rcsf</td>
<td>7</td>
<td>6.07</td>
<td>0.0220</td>
</tr>
<tr>
<td>Incstage, date</td>
<td>3</td>
<td>6.17</td>
<td>0.0209</td>
</tr>
<tr>
<td>Species, rcsf</td>
<td>6</td>
<td>7.72</td>
<td>0.0096</td>
</tr>
<tr>
<td>Date</td>
<td>2</td>
<td>8.04</td>
<td>0.0082</td>
</tr>
<tr>
<td>Species, incstage, date, rcsf</td>
<td>8</td>
<td>8.17</td>
<td>0.0077</td>
</tr>
<tr>
<td>Species, incstage</td>
<td>6</td>
<td>10.14</td>
<td>0.0029</td>
</tr>
<tr>
<td>Species, incstage, date, rcsf, incstage (\times) rcsf</td>
<td>9</td>
<td>10.36</td>
<td>0.0026</td>
</tr>
<tr>
<td>Species</td>
<td>5</td>
<td>11.38</td>
<td>0.0015</td>
</tr>
<tr>
<td>Species, incstage, date</td>
<td>7</td>
<td>12.18</td>
<td>0.0010</td>
</tr>
<tr>
<td>Species, incstage, date, species (\times) date, rcsf</td>
<td>12</td>
<td>12.34</td>
<td>0.0010</td>
</tr>
<tr>
<td>Species, date</td>
<td>6</td>
<td>13.48</td>
<td>0.0005</td>
</tr>
<tr>
<td>Species, rcsf, species (\times) rcsf</td>
<td>10</td>
<td>14.26</td>
<td>0.0044</td>
</tr>
<tr>
<td>Species, incstage, date, species (\times) date</td>
<td>11</td>
<td>17.38</td>
<td>(8 \times 10^{-5})</td>
</tr>
<tr>
<td>Species, date, species (\times) date</td>
<td>10</td>
<td>17.60</td>
<td>(7 \times 10^{-5})</td>
</tr>
<tr>
<td>Species, incstage, date, rcsf, species (\times) incstage</td>
<td>12</td>
<td>22.10</td>
<td>(7 \times 10^{-6})</td>
</tr>
<tr>
<td>Species, incstage, species (\times) incstage</td>
<td>10</td>
<td>22.32</td>
<td>(7 \times 10^{-6})</td>
</tr>
<tr>
<td>Species, incstage, date, rcsf, species (\times) incstage, incstage (\times) rcsf</td>
<td>13</td>
<td>25.86</td>
<td>(1 \times 10^{-6})</td>
</tr>
</tbody>
</table>

Note: Number of parameters \((K)\), difference in Akaike’s information criterion adjusted for small sample size \((\Delta AIC_c)\), and Akaike weights \((w_i)\). Variables are species, incstage (early or late incubation), date (julian date), rcsf (clutch size adjusted for laying date).

* \(AIC_c\) of the top model was 467.85.
accounted for >90% of the total candidate model weights, so we did not need to utilize model averaging techniques (Burnham and Anderson 2002). Probability of abandonment was highest for early-laying nests, followed by late-laying nests, and was lowest for incubation-stage nests. According to odds ratios, early-laying females were 7.04 (5.06–9.78) times more likely to abandon nests than were incubating females, and late-laying females were 1.93 (1.37–2.72) times more likely to abandon nests than were incubating females.

Mallards and Blue-winged Teal exhibited a greater probability of nest abandonment later in the season, whereas Northern Shovelers, Gadwall, and Northern Pintails exhibited a decline in probability of nest abandonment with later date, and this pattern was especially pronounced among Northern Pintails (Fig. 1). At the median nesting date for the entire study (30 May), predicted abandonment probabilities were 0.090 for Mallards, 0.051 for Northern Shovelers, 0.047 for Blue-winged Teal, 0.045 for Gadwall, and 0.036 for Northern Pintails. Because of the complexity of our best model, we have also included a table of the overall proportions of nests abandoned by nest age and species (Table 4).

When incubation-stage nests were analyzed separately, several models performed well. The top five models composed >90% of the total model weights (Table 3), which were averaged (Burnham and Anderson 2002) to obtain parameter estimates and 95% confidence intervals. Four models contained date-adjusted clutch size, three models contained incubation stage, and two models contained date.

The odds ratio for incubation stage was 1.38 (1.00–1.89), which suggested that, on average, early-incubation nests were 38% more likely to be abandoned than were late-incubation nests. The odds estimate for date-adjusted clutch size was 0.81 (0.70–0.95), which suggested that a female was 19% less likely to abandon her nest for every additional egg in her completed clutch. The odds estimate for date was 0.996 (0.903–1.097). Thus, we concluded that date has little influence on the probability of abandonment of incubation-stage nests, despite its appearance in two of the top models for incubation-stage nests (Table 3).

Since abandonment probability increased with nest age, we wanted to compare our observed results with the values predicted if females abandoned nests solely based on the benefit expected from the nest at the age (laying days + incubation days) it was found. We modeled expected benefits of incubation-stage nests given that

\[
\text{Expected benefits}_{\text{lay/ incubation}} = \frac{P_{a1}}{P_{a2}} = \text{dsr}^{a2-a1}
\]

Based on the mean ages at which our nests were abandoned within each nest age category, we calculated the proportional differences in expected benefits among age categories. Thus, early-laying nests have 59% of the expected benefits of incubation-stage nests given that

\[
\text{Expected benefits}_{\text{late/ incubation}} = \frac{P_{a1}}{P_{a2}} = 0.964^{16.6–2.4} = 0.59
\]

Late-laying nests have 73% of the expected benefits of incubation-stage nests given that

\[
\text{Expected benefits}_{\text{early/ incubation}} = \frac{P_{a1}}{P_{a2}} = 0.964^{16.6–7.9} = 0.73
\]

Lastly, nests found during early incubation have 71% of the expected benefits of those found during late incubation given that

\[
\text{Expected benefits}_{\text{early/ late}} = \frac{P_{a1}}{P_{a2}} = 0.964^{23.6–14.2} = 0.71
\]

Abandonment probability owing to the expected benefits conferred by nest age is predicted to be inversely proportional to nest age. Early-laying nests have 59% (eq. 3) of the expected benefits of incubation-stage nests, so they should be abandoned 1.69 (1/0.59) times as often. A nest found during late laying has 73% (eq. 4) of the benefits expected from an incubation-stage nest, and thus should be abandoned 1.37 (1/0.73) times as often. These predicted values are lower than our observed values of 7.04 (5.06–9.78) and 1.93 (1.37–2.72) for early-laying and late-laying nests, respectively, relative to incubation-stage nests. That is, during laying, females abandoned nests more frequently than predicted by the expected benefits from current reproduction hypothesis.

Nests found during early incubation have 71% of the expected benefits of late-incubation nests (eq. 5), so the expected benefits hypothesis predicts that they should be abandoned 1.41 (1/0.71) times as often. Our nests were 1.38 (1.00–1.89) times more likely to be abandoned if found during early rather than late incubation. Thus, incubating females’ pattern of abandonment probability was similar to that predicted by the expected benefits hypothesis.

Discussion

Parental investment is any effort that increases the offspring’s chance of survival at the cost of a parent’s ability to invest in other offspring (Trivers 1972). Continuing to
tend a nest can limit (or eliminate, in the case of her death) a female duck’s ability to invest in future offspring, yet there is no benefit from an abandoned nest (Armstrong and Robertson 1988). Therefore, patterns of nest abandonment would be expected to follow predictions based on parental investment theory, and if they do not, then they might provide impetus for altering these hypotheses.

Year–site specific nest success, used as a surrogate for predator activity and ultimately for risk of predation, apparently did not affect nest abandonment because it did not appear in the best models. We think that this was a good, direct test for the effects of predators because year–site specific nest success was quite variable (range = 4%–56%). Perhaps nesting females either cannot detect predators or do not react to their presence by abandoning nests more frequently. By contrast, ducks that are repeatedly flushed by humans (an indirect test) decrease their risk-taking behavior (Mallory et al. 1998; Forbes et al. 1994; Gunness and Weatherhead 2002), flushing from progressively greater distances when approached. It is possible that nesting ducks respond differently to nest predators than they do to human investigators.

The interaction between species and nest initiation date made the effects of these factors difficult to interpret. Results for Northern Pintails, Northern Shovelers, and Gadwall were consistent with the renesting (within season) component of the future reproduction hypothesis. Abandonment probabilities for Northern Pintails were initially high, but declined very rapidly, which may reflect strong seasonal declines in renesting (Grand and Flint 1996; Guyn and Clark 2000; Richkus 2002), especially when wetland conditions deteriorate (Richkus 2002). In particular, breeding Northern Pintails tend to settle in areas with temporary wetlands that quickly dry up in the absence of rain.

Results for Mallards and Blue-winged Teal were consistent with the expected benefits hypothesis, which predicts higher abandonment probabilities late in the nesting season when the expected benefits from the nest are low because
of poor survival of late-hatched broods (Orthmeyer and Ball 1990; Rotella and Ratti 1992; Dzus and Clark 1998), as well as the next breeding season component of the future reproduction hypothesis. Given their relatively high survival probabilities, coupled with their high nesting propensity, abandoning a late-season nest in favor of increased survival to and reproduction in the following year makes sense for Mallards. But Blue-winged Teal are small-bodied with a low nesting propensity, so their prospects for surviving and breeding the next season are comparatively lower. Blue-winged Teal (Anas discors) nest relatively late and are the earliest fall migrants of the species that we studied (Rohwer et al. 2002). Perhaps they abandon late-season nests frequently, despite having life-history traits that would predict consistently low abandonment, because of this time-bind for females and young. A young brood abandoned early by a female leaving to molt and migrate would have low survival anyway (Orthmeyer and Ball 1990; Rotella and Ratti 1992; Dzus and Clark 1998; Krapu et al. 2000); thus, by abandoning at the nesting stage, she may in essence “cut her losses”.

Mallards and Blue-winged Teal exhibited the same seasonal pattern, therefore a comparison between them was informative. Of the species we studied, they represent the extremes of life-history strategy and nesting propensity. As predicted by the future reproduction hypothesis, Mallards (a large-bodied, prolific renester; Rotella et al. 1993; Paquette et al. 1997; Arnold et al. 2010) exhibited a consistently higher probability of abandonment (Fig. 1) than did Blue-winged Teal (the smallest and least likely to renest; Strohmeyer 1967). These results are consistent with those of Forbes et al. (1994), in which laying Mallards abandoned 32.5% of nests compared with 20.9% for Blue-winged Teal. However, abandonment probability did not differ among species during incubation (Tables 3, 4), which is also consistent with the findings of Forbes et al. (1994). We think that finding species-specific patterns consistent with the future reproduction hypothesis during laying but not incubation is one key to an overall understanding of dabbling duck nest abandonment, as the predictions based on species are unequivocal.

When we examined all nests, evidence from nest-stage-specific patterns was consistent with the hypothesis that abandonment probabilities are positively related to opportunities for future reproduction. Younger nests were more likely to be abandoned especially during the early-laying (<5 egg) stage, which is consistent with the prediction that females with greater opportunity to renest in a given year would abandon more frequently. Moreover, relative to incubation-stage nests, early-laying nests were 4 times more likely to be abandoned than predicted based on the expected benefit of the nest based on its age. The same pattern was observed in late-laying nests, albeit to a much lesser degree. However, though abandonment probability was higher if the nest was found during early rather than late incubation (see also Ackerman and Eadie 2003; Ackerman et al. 2003), the observed difference was similar to the magnitude predicted if age-related expected benefits from the nest were the only influence. The overall pattern relative to nest age suggests that opportunity for future reproduction has a substantial effect on dabbling duck nest abandonment during laying, particularly early laying, but during incubation, evidence is consistent with the effects of the expected benefit from the nest.

Indeed, the probability of abandonment during incubation decreased with higher relative clutch size, which also supported the expected benefits hypothesis. We realize that the clutch size effect that we observed could also be due to females’ prior investment in the clutch leading to reduced future reproductive potential (Sargent and Gross 1985; Ackerman and Eadie 2003). However, we find little to suggest that egg-laying is particularly costly for temperate-nesting ducks, except that it exposes them to additional risk of predation (Arnold et al. 1987; Arnold and Rohwer 1991). Yet even this risk should be minimal, because females attend laying-stage nests only during daylight hours (Gloutney et al. 1993; Loos and Rohwer 2004) when most mammalian predators are inactive.

Nonetheless, we cannot decouple the effects of expected benefits and future reproductive opportunities relative to clutch size based on our study. However, Ackerman and Eadie (2003) used egg mortality data to model the benefits expected from Mallard clutches at different points during incubation, then manipulated clutch sizes to equalize expected benefits from early- and late-incubation-stage nests with different prior investment. Abandonment probability increased with the severity of clutch removal (reduced expected benefits) rather than the degree of prior investment (future reproduction). Severity of clutch size loss (by predators) or experimental removal also influenced nest abandonment in other studies (Armstrong and Robertson 1988, Ackerman et al. 2003). In sum, ours and previous studies have reported evidence consistent with the influence of expected benefits from the nest during incubation, and no unequivocal evidence to suggest that future reproduction plays a role during incubation.

However, we think this tells only part of the story. Only our study and Forbes et al. (1994) examined both laying- and incubation-stage nests, and in both cases, species and nest age patterns were consistent with the future reproduction hypothesis but only during the laying period (although Forbes et al. (1994) only made the single comparison between laying- and incubation-stage nests). Thus, we propose a two-stage model for explaining parental investment by nesting dabbling ducks, in which opportunity for future reproduction is the predominant influence during laying, likely because of renesting propensity. However, once incubation has begun, the expected benefits from the nest appear to have the greatest (if not the only) influence.

Expected benefits may also play a role during laying, but its influence is apparently dwarfed by opportunities for future reproduction during early laying when renesting propensity is high, likely because the female still possesses a set of developing follicles (Arnold et al. 2010). In fact, the sharpest drop in abandonment probability occurred between early-laying and late-laying nests, not between late-laying and incubation, as we expected. Late-laying females likely still possess enough developing follicles to either complete a full clutch or begin a second nest if the current one is destroyed or abandoned. However, with each egg laid, female ducks spend increasing amounts of time on the nest (Loos and Rohwer 2004), and by late-laying, begin to exhibit behavior (e.g., adding down to the nest; Glover 1956) and
undergo some of the hormonal changes (Bluhm 1992) associated with incubation. Late in laying, perhaps parental care decisions that earlier were based largely on opportunities for future reproduction are shifting to an assessment based on the expected benefits from the nest; hence the intermediate abandonment probability.

Additional research on abandonment of laying-stage nests in a variety of species would be a good test for our ideas, and large, multispecies data sets, such as the Northern Prairie Nest Data Center (Northern Prairie Wildlife Research Center 2001), would lend themselves to such analyses. Adding or removing eggs from laying-stage nests to equalize expected benefits during different laying stages would likely be impractical because the laying period is relatively short. Moreover, such an experiment would require repeated disturbance of nests during laying, especially early when abandonment probabilities are high.

We were unable to test for some factors, such as female age and prior (within season) nestling attempts, that might influence abandonment probability, perhaps by influencing renesting propensity and clutch size. In Mallards, after second year (ASY) females have a higher probability of renesting than second year (SY) birds, and renesting probability declines with increased number of previous nest attempts (Arnold et al. 2010). In particular, these factors could be correlated with the seasonal abandonment patterns that we observed because ASY females tend to nest earlier and lay larger clutches (reviewed in Rohwer 1992), and because later nests have a higher probability of being renests. However, clutch sizes do not differ among first nests and renests if clutch size is adjusted for laying date (Richkus 2002; Arnold et al. 2010), which we did.

Our findings suggest some practical guidelines for research and management. To avoid causing nest abandonment, researchers should avoid disturbing early-laying females, which attend nests early in the morning (Gloutney et al. 1993; Loos and Rohwer 2004). Mallards make particularly poor research subjects if protocols require disturbing early-laying females, as more than 25% of these nests were abandoned. Investigators might choose to avoid searching very early in the season for Northern Pintails, and very late in the season for Blue-winged Teal and Mallards, because abandonment was high during these periods.

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