

Factors affecting conspecific brood parasitism in Wood Ducks *Aix sponsa* of the intermountain region of western North America

KONRAD HAFEN^{1*} & DAVID N. KOONS²

¹Department of Watershed Sciences, Utah State University, 5210 Old Main Hill,
Logan, Utah 84322, USA.

²Department of Wildland Resources and The Ecology Center, Utah State University,
5230 Old Main Hill, Logan, Utah 84322, USA.

*Correspondence author. E-mail: khafen74@gmail.com

Abstract

The installation of artificial nest boxes has frequently been used as a management measure to increase breeding habitat and thus bolster Wood Duck *Aix sponsa* populations. However, Wood Duck populations that rely heavily on nest box programmes are also prone to increased frequency of intense conspecific brood parasitism (CBP), which can reduce egg hatchability and increase rates of nest abandonment among hosts. In 2010, 2012 and 2013 we monitored 95–110 nest boxes in northern Utah, USA, for intense CBP (clutches with ≥ 16 eggs). Using logistic regression and information-theoretic methods, we compared the influence of nest box visibility, proximity to other nest boxes, and proximity to aquatic habitat on the probability of a Wood Duck nest being intensely parasitized by a conspecific female. Our data indicated that a combination of nest box mount type and wooded habitat cover were the main drivers of intense CBP, with the odds of intense CBP increasing by a factor of 9.0 for boxes mounted on a pole in wooded areas, and by a factor of 20.8 for boxes mounted on a pole in open areas, when these were compared with CBP in boxes mounted on trees in wooded areas. The results agreed with hypotheses that tree-mounted boxes in wooded habitat offer more concealment for nesting females as they enter and leave nests, making their nests less likely to be exploited by prospecting parasites. Placing Wood Duck nest boxes in trees, where possible, might thus decrease the occurrence of intense CBP and the negative impact it can have on the fitness of the host.

Key words: *Aix sponsa*, GIS, hatching success, intra-specific interaction, nest box, nest parasite.

In response to over-harvest of Wood Ducks *Aix sponsa* in the early 1900s, many programmes have been initiated to bolster Wood Duck breeding habitat by erecting artificial nest boxes, and the efficacy of such programmes has been well documented (Bellrose *et al.* 1964; Doty & Kruse 1972; Dugger & Fredrickson 1992). However, even in the presence of an effective nest box programme, other factors can prevent Wood Duck populations from meeting management objectives. For example, predation, primarily from the Common Raccoon *Procyon lotor*, can limit population growth even when sufficient nest sites exist (Strange *et al.* 1971; Robb & Bookhout 1995). Furthermore, inter- and intra-specific competition for available nest sites might exclude breeding individuals from preferred nesting habitat (McGilvrey & Uhler 1971; Newton 1994; Semel & Sherman 2001). Increased competition between conspecifics in conjunction with limited nest site availability can also increase the occurrence of brood parasitism (Semel & Sherman 2001; Nielsen *et al.* 2006a; Lyon & Eadie 2008).

Wood Ducks frequently engage in facultative conspecific brood parasitism (CBP; Yom-Tov 1980, 2001), which is known to occur across all levels of nest-site scarcity (Morse & Wight 1969; Semel & Sherman 2001). For populations nesting primarily in natural cavities, parasitized clutches generally have ≤ 12 –16 eggs (Ryan *et al.* 1998; Nielsen *et al.* 2006b), equivalent to the expected maximum clutch size for an individual female (Heusmann 1972; Semel & Sherman 1992). In many instances, however, Wood Duck populations relying on artificial

boxes for nesting habitat frequently lay larger clutches (Semel *et al.* 1988; Semel & Sherman 1992; Hartke *et al.* 2006). As the level of CBP in a nest exceeds the natural clutch size, hatchability of the clutch decreases and the likelihood of the female abandoning the nest increases (Heusmann 1972; Semel *et al.* 1988; Semel & Sherman 1992, 2001; Nielsen *et al.* 2006a,b). Furthermore, intensely parasitized nests (*i.e.* with clutches of ≥ 12 –16 eggs) take longer to incubate, resulting in greater predation risk both for the eggs and for the incubating female because of the prolonged sedentary period (Hartke *et al.* 2006), additional energy expenditure by the female, and a reduction in the hatchability of host eggs (Hepp *et al.* 1990; Nielsen *et al.* 2006a). Frequent occurrence of intense CBP in a population can thus decrease reproductive success, and is a concern for Wood Duck populations relying largely on artificial nest boxes (Jones & Leopold 1967; Clawson *et al.* 1979).

The occurrence and intensity of CBP are thought to be dictated primarily by nest visibility and density, which directly affect the ability of prospecting parasitic females to locate host nests (Heusmann *et al.* 1980; Rohwer & Freeman 1989; Semel & Sherman 1995). For Wood Ducks, it is believed parasitic females generally locate host nest sites by observing a nesting female entering or leaving a nest cavity, and thus cases of intense CBP in artificial nests may be attributed to the visibility and density of nest boxes (Semel & Sherman 1995; Nielsen *et al.* 2006a). For logistical purposes, traditional nest box programmes have often involved mounting nest boxes on poles over

or near water at high densities surrounding a water feature, rendering the nests highly susceptible to CBP because of the relative ease with which parasitic females can find host nest sites (Semel & Sherman 1995; Rohwer & Freeman 1989). Boxes closer to water have also been observed to have higher rates of CBP because more Wood Ducks occur in these areas (Ryan *et al.* 1998).

From an applied standpoint, managers benefit from understanding both the ecological and evolutionary mechanisms affecting CBP to identify the factors limiting reproductive success at the population level. Given the ability of nest boxes to mitigate for habitat loss, reduce predation risk and decrease competition for nest sites, improving reproductive efficiency is a logical next step for artificial Wood Duck nest box programmes. Earlier studies have already provided evidence that mounting nest boxes in trees limits their visibility, and that placing the boxes at natural densities can reduce the frequency of extreme clutch sizes (Semel & Sherman 1986, 1992, 1995, 2001). More recently, Nielsen *et al.* (2006b) highlighted the importance of examining more closely the relationship between habitat and intense CBP, with a view to improving the efficacy of nest box programmes.

The aforementioned studies were conducted, however, in regions of North America where forest and woodland cover is relatively common. In the intermountain region of western North America, peripheral Wood Duck populations occur in valleys where cottonwood *Populus angustifolia* and *P. fremontii* gallery forests have all but disappeared as a result of urbanisation and reduced water tables (Poff *et al.* 2011).

Because of these changes, and landscapes that are naturally more open than in other parts of the Wood Duck's breeding range, there are few natural cavities and few locations to "conceal" an artificial nest box. Factors affecting CBP in more forested parts of the Wood Duck breeding range might thus be weaker in the intermountain region of North America. To test this prediction, we examined the influence of nest box visibility, proximity to other nest boxes, and proximity to aquatic habitats on the probability of intense CBP in northern Utah. By providing further knowledge about the factors affecting intense CBP, managers can better develop programmes to bolster Wood Duck populations in the intermountain region of western North America, and elsewhere.

Methods

Study area

Cache Valley is a large elevated valley (~1,300–1,500 m elevation), dominated by agricultural use with one large urban area (Logan City), located in northern Utah and southern Idaho, USA (Fig. 1). The valley is bounded by high elevation mountains (~2,500–3,000 m) on the east and west, from which tributary waters flow to the regionally important Bear River. Several of these tributaries entwine the valley with narrow riparian corridors dominated by Narrowleaf Cottonwood *Populus angustifolia*, willow (namely *Salix amygdaloides* and *S. fragilis*), Boxelder *Acer negundo*, and Russian-olive *Eleagnus angustifolia* trees in the overstorey, and bulrush *Scripus* sp. and cattail *Typha* sp. in the emergent wetlands.

Additionally, some lowland riparian and wetland habitats are present in the mountains bounding the valley. Our study area was restricted to the Utah portion of Cache Valley (Fig. 1) and was selected to monitor the effects of a nest box programme initiated by The Utah Waterfowl Alliance in 2010 to increase the abundance of Wood Ducks in the area.

Field methods

Nest boxes were installed prior to the 2010 breeding season, in wooded riparian areas where possible, but with many being installed in open agricultural fields near water features. Boxes were mounted either on trees (where available) or on metal poles 127–254 mm in diameter. Upon installation of each box we recorded if the box was

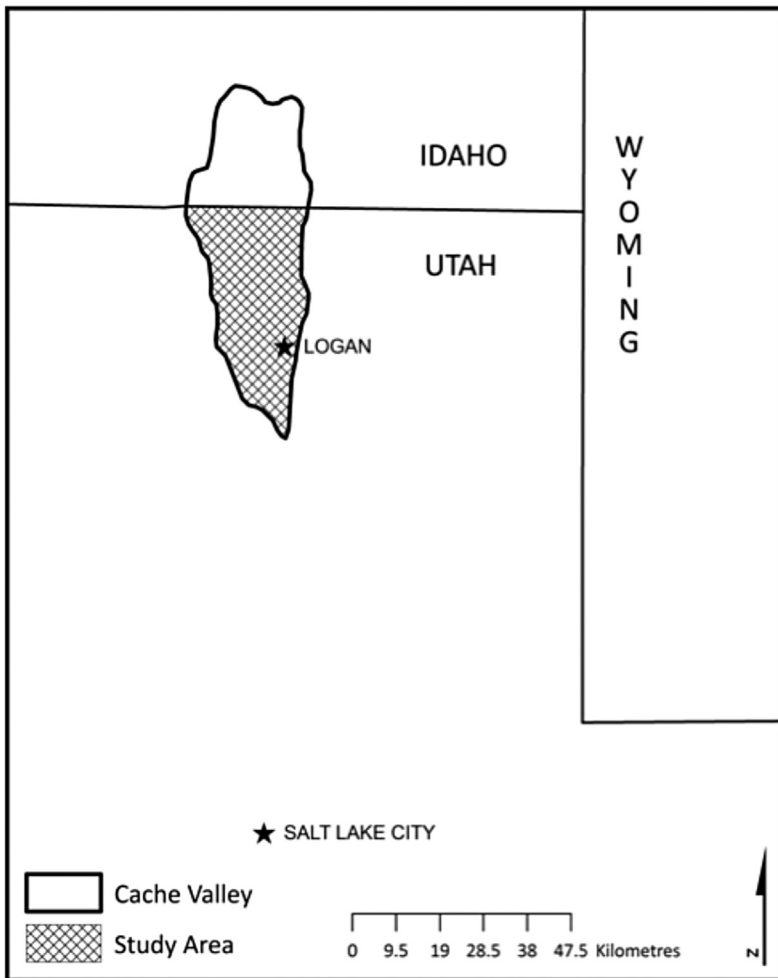


Figure 1. Location of the Cache Valley, Utah, USA study area.

located in an open or wooded habitat, the type of box (wood or plastic), and the prominent water feature nearest the box. We monitored nest boxes for occupancy by nesting Wood Duck females between 15 April and 15 July in 2010, 2012 and 2013. Exceptionally high run-off in 2011 rendered most nest boxes inaccessible during the nesting season. Between these dates we examined each nest box a minimum of three times. From a sample of approximately 150 boxes located in riparian and wetland habitats, 110, 95 and 98 boxes were monitored in 2010, 2012 and 2013, respectively. At each visit, occupancy, species and the number of eggs present were recorded. We also noted if the nest had hatched or been abandoned. If a bird flushed or was observed in the box, or evidence of nesting (eggs, feathers) was observed, we classified the box as occupied. As our focus in this study was to examine factors that influenced the probability of intense CBP by Wood Ducks, we focused on the sample of nests where incubation was initiated (partial clutch loss should be minor given that nests were concealed in a box and the primary predator, raccoon, tends to take all of the eggs when depredating a nest; Bellrose *et al.* 1964). Data recorded during visits were summarised for each nest box to include only the maximum number of eggs in each clutch. We classified clutches with ≥ 16 eggs as occurrences of intense CBP (Semel & Sherman 1986; Nielsen *et al.* 2006b).

Covariate predictors of brood parasitism

To test our prediction that factors previously shown to affect CBP in forested

parts of the Wood Duck's breeding range may differ or be weaker in more open landscapes of the intermountain region of North America, we identified five explanatory variables that describe nest box visibility and density. Variables were obtained from direct observation during nest box installation, or from subsequent GIS analyses of relationships between nest boxes and the landscape. The variables we considered were mount type (M ; on a tree or metal pole), if the nest box was located in wooded habitat or open areas (W , a binary variable), distance from one nest box to the nearest neighbouring nest box (D_{BOX} , in metres), distance from the nest box to water (D_{WAT} , in metres), and the number of other nest boxes located within 100 m (C_{100}). Since all tree-mounted boxes were located in wooded areas, W becomes confounded with M when included together in a model. In order to separate the effect of mount type from the effect of habitat to the best of our ability, we therefore constructed a variable (X_{MW}) with all possible mount type and box location categories: pole-mounted in open areas, pole-mounted in wooded areas and tree-mounted in wooded areas.

Data analysis

Logistic regression models were constructed to examine effects of the explanatory variables described above on the probability of intense CBP within our study area. Univariate effects of M , W , X_{MW} , D_{BOX} , D_{WAT} and C_{100} were considered, as well as the additive effects of D_{BOX} , D_{WAT} and C_{100} with both M and X_{MW} . However, we did not consider additive effects of M and W in

relation to each other because of the reason described above. There was no evidence for multicollinearity between any pair of explanatory variables. In all, we constructed 12 models and compared them using Akaike’s Information Criterion adjusted for sample size (AIC_c ; Table 1). The deviation in a model’s AIC_c score from the top model (ΔAIC_c) was used to assess the relative support among models, given the available data (Burnham & Anderson 2002). All analyses were conducted in R version 3.1.1 (R Development Core Team 2014).

Results

Relevant data were obtained from 44, 43 and 20 clutches in 2010, 2012 and 2013 respectively, with 23, 15 and 1 intensely parasitized nests recorded in these years. Overall, a greater percentage of tree-mounted boxes (52.9%, 70.6% and 28.6%) were occupied than pole-mounted boxes (28.0%, 46.2% and 22.6%) in each year of the study.

Among the models considered to explain variation in intense CBP among Wood Duck

Table 1. Models examining effects of woodland/open site (W), tree/pole mount (M), distance to water (D_{WAT}) and nearest box (D_{BOX}), number of boxes within 100 m (C_{100}) and M/W combinations (X_{MW}) on intense conspecific brood parasitism for Wood Duck breeding in the Cache Valley, Utah (abbreviations are as described in the text). The degrees of freedom (d.f.) denote the number of parameters in the model, ΔAIC_c is the difference between the AIC_c for a given model and that of the top model, and “Model weight” is the Akaike weight which represents the relative likelihood of each model.

Model	d.f.	ΔAIC_c	Model weight
X_{MW}	3	0.0	0.199
M	2	0.5	0.155
$X_{MW} + D_{WAT}$	4	0.6	0.148
$M + D_{WAT}$	3	0.7	0.140
$X_{MW} + C_{100}$	4	1.5	0.094
$X_{MW} + D_{BOX}$	4	1.8	0.081
$M + C_{100}$	3	1.9	0.077
$M + D_{BOX}$	3	2.2	0.066
W	2	3.3	0.038
D_{BOX}	2	15.5	0.000
D_{WAT}	2	15.9	0.000
C_{100}	2	16.3	0.000

next boxes on our study area, M and X_{MW} were most supported by the data (Table 1). Although other models had $\Delta AIC_c < 2$, these were more complex versions of the top models that included M or X_{MW} , thus indicating that these additional variables were uninformative because they resulted in higher, not lower, AIC_c values (Arnold 2010). When considering model M , the odds of experiencing intense CBP increased by a factor of 17.2 (95% C.I. = 3.4–314.2) for boxes mounted on a pole relative to boxes mounted in a tree (Fig. 2). When considering the effect of both mounting type and wooded habitat (X_{MW}), the odds of intense CBP increased by a factor of 9.0 (95% C.I. = 1.3–178.6) for pole-mounted boxes in

wooded areas and by a factor of 20.8 (95% C.I. = 4.0–381.4) for pole-mounted boxes in open areas, relative to tree-mounted nest boxes in wooded areas (Fig. 2). We additionally considered a 14 egg threshold for defining intense CBP, but all results were qualitatively similar to the 16 egg threshold and are thus not presented here.

Discussion

In concurrence with other studies (*e.g.* Semel & Sherman *et al.* 1986, 1992, 1995, 2001; Nielsen *et al.* 2006a), we found that mounting method, and a combination of mounting method and habitat, had the greatest effect on the frequency of intense CBP, with higher frequencies recorded for

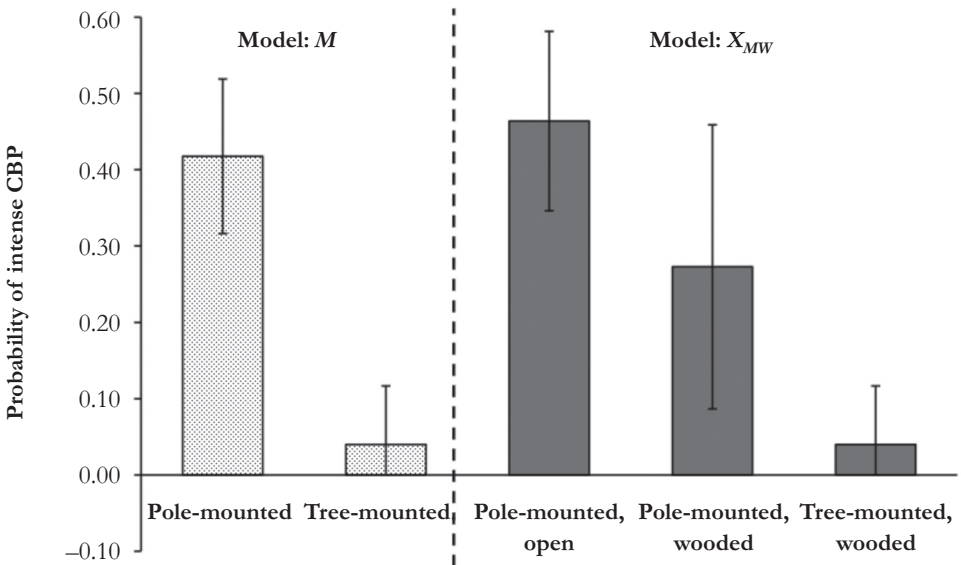


Figure 2. Estimates and 95% confidence intervals of the probability of intense CBP as predicted by our top two models. The nest box mount type (on a pole or in a tree) is described by model M , and the X_{MW} model combines the effect of habitat cover with mounting type (pole-mounted in and open area, pole-mounted in a wooded area, or tree-mounted in a wooded area). Predictions for the two models are separated by the dashed line.

pole-mounted boxes and also for boxes mounted in open areas (Table 1; Fig. 2). Unlike other studies (Semel & Sherman 1995; Ryan *et al.* 1998; Nielsen *et al.* 2006a), however, we did not find evidence for a relationship between intense CBP and nest box proximity, nest box density or the distance from the nest box to water. The results thus provide partial support for our prediction that factors affecting intense CBP in the intermountain region of North America may differ from those in more forested parts of Wood Duck breeding range.

Semel and Sherman's (1995) study in northeast Illinois also identified nest boxes mounted on poles as being more frequently parasitized by conspecifics compared to nest boxes mounted in trees. Given that pole-mounted boxes are generally placed in areas where trees are not available for mounting, they are believed to receive greater CBP because they are more visible and parasitic females locate these nests more readily as they observe host females entering and leaving their nest box (Rohwer & Freeman 1989; Semel & Sherman 1995; Nielsen *et al.* 2006b). Although the X_{MW} model provided evidence that installing nest boxes in wooded habitat decreased the occurrence of intense CBP in wooded areas of the Cache Valley, our results clearly indicated that it was mounting boxes on trees that had the strongest effect of lowering the probability of nest boxes experiencing intense CBP. This could result from greater concealment offered by surrounding vegetation or concealment offered by the tree itself. For example, pole-mounted boxes (even those in wooded areas) are visible from all angles (if the observer is close enough), whereas

tree-mounted boxes are not visible from behind.

Despite the apparent concealment of tree-mounted boxes, they experienced greater occupancy than pole-mounted boxes, indicating that the ability of Wood Ducks to find these nest box sites is not determined by their location or visibility. This suggests that nesting females do not have more difficulty locating tree-mounted boxes, but that the tree may conceal the host's entry and exit so they are less easily detected as an occupied nest by prospecting parasitic females (Heusmann *et al.* 1980; Rohwer & Freeman 1989; Semel & Sherman 1995). However, occupancy of these sites may also be attributed to nest height rather than to nest location or visibility. Bellrose *et al.* (1964) and Lacki *et al.* (1987) determined that, for both natural and artificial nest sites, those higher above the ground were preferable to those at lower levels. Our pole-mounted boxes were rarely over 2 m from the ground and never exceeded 2.5 m (allowing observation without a ladder), whereas most tree-mounted boxes were over 2 m from the ground.

In contrast to Clawson (1975) and Heusmann *et al.* (1980), we did not find that nest box density within a 50 m or 100 m radius of a nest affected the probability of intense CBP, nor did we find an influence of distance to the nearest neighbouring box (Table 1). However, every nest box in our study had at least one other box located within 50 m. Thus, we cannot entirely eliminate the possibility that nest box density and proximity had an effect on CBP during our study. Despite these nest box placement densities, tree-mounted boxes

still had a lower probability of parasitism. If this is the case, it might be possible to place tree-mounted boxes at higher densities than pole-mounted boxes without experiencing the same negative rates of intense CBP. Contrary to other observations, occurrence of intense CBP decreased over the course of our study. A possible explanation is that the population expanded spatially to take advantage of newly installed boxes at the periphery of the study area, decreasing the overall density of the Wood Duck population in the study area. Also, box occupancy was lower in 2013 than in 2010 and 2012, perhaps making it more difficult for parasites to locate hosts, or decreasing competition for available nest sites.

While artificial nest box programmes can be effective tools for increasing Wood Duck breeding populations in areas where habitat loss limits availability of natural nest sites (Bellrose *et al.* 1964; Doty & Kruse 1972; Dugger & Fredrickson 1992), we suggest that the placement of nest boxes can be improved to reduce CBP and potentially improve egg hatchability. Our results are echoed by others (*e.g.* Semel *et al.* 1988; Semel & Sherman 1995; Hartke & Hepp 2004), providing strong evidence that to minimise the probability of intense CBP, nest boxes should be mounted in trees rather than a variety of artificial mounting habitats, even in the open landscapes found throughout the intermountain region of North America. However, while box placement is an important factor for minimising intense CBP, it is only one of many considerations managers must make when implementing nest box programmes, and all factors with the potential to influence

Wood Duck population trends should be considered carefully (Eaton 1966; Haramis & Thompson 1985; Robb & Bookhout 1995).

Acknowledgements

This research was conducted as part of an undergraduate research project. Support and materials were provided by TUWA. We thank Carl Taylor, Dillon Hoyt and Jason Carlisle for assistance with study design and implementation, as well as B. Dugger and J. Eadie for comments on a previous version of the manuscript. Monitoring and handling of nests and animals was done under Utah COR 2BAND8301 and IACUC protocol 2128.

References

- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74: 1175–1178.
- Bellrose, F.C., Johnson, K.L. & Meyers, T.U. 1964. Relative value of natural cavities and nesting houses for wood ducks. *Journal of Wildlife Management* 28: 661–676.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: Second Edition*. Springer-Verlag, New York, USA.
- Clawson, R.L. 1975. The ecology of dump nesting in wood ducks. M.Sc. thesis, University of Missouri, Columbia, USA.
- Clawson, R.L., Hartman, G.W. & Fredrickson, L.H. 1979. Dump nesting in a Missouri wood duck population. *Journal of Wildlife Management* 43: 347–355.
- Doty, H.A. & Kruse, A.D. 1972. Techniques for establishing local breeding populations of wood ducks. *Journal of Wildlife Management* 36: 428–435.
- Dugger, K.M. & Fredrickson, L.H. 1992. 13.1.6. Life history and habitat needs of the Wood

- Duck. In D.H. Cross & P. Vohs (eds.), *Waterfowl Management Handbook*, Paper 38. U.S. Fish and Wildlife Service, Fort Collins, Colorado, USA. Available on-line at <http://digitalcommons.unl.edu/icwdmwfm/38> (last accessed 31 May 2016).
- Eaton, R.L. 1966. Protecting metal wood duck houses from raccoons. *Journal of Wildlife Management* 30: 428–430.
- Hartke, K.M. & Hepp, G.R. 2004. Habitat use and preferences of breeding female wood ducks. *Journal of Wildlife Management* 68: 84–93.
- Hartke, K.M., Grand, J.B., Hepp, G.R. & Folk, T.H. 2006. Sources of variation in survival of breeding female wood ducks. *The Condor* 108: 201–210.
- Haramis, G.M. & Thompson, D.Q. 1985. Density-production of wood ducks in a northern greentree impoundment. *Journal of Wildlife Management* 49: 429–436.
- Hepp, G.R., Kennamer, R.A. & Harvey IV, W.F. 1990. Incubation as a reproductive cost in female wood ducks. *The Auk* 107: 756–764.
- Heusmann, H.W. 1972. Survival of wood duck broods from dump nests. *Journal of Wildlife Management* 36: 620–624.
- Heusmann, H.W., Bellville, R. & Burrell, R.G. 1980. Further observations on dump nesting by wood ducks. *Journal of Wildlife Management* 44: 908–915.
- Jones, R.E. & Leopold, A.S. 1967. Nesting interference in a dense population of wood ducks. *Journal of Wildlife Management* 31: 221–228.
- Lacki, M.J., George, S.P. & Viscosi, P.J. 1987. Evaluation of site variables affecting nest box use by wood ducks. *Wildlife Society Bulletin* 15: 196–200.
- Lyon, B.E. & Eadie, J.M. 2008. Conspecific brood parasitism in birds: a life-history perspective. *Annual Review of Ecology, Evolution, and Systematics* 39: 343–363.
- McGilvrey, F.B. & Uhler, F.M. 1971. A starling-deterrent wood duck nest box. *Journal of Wildlife Management* 35: 793–797.
- Morse, T.E. & Wight, H.M. 1969. Dump nesting and its effect on production in wood ducks. *Journal of Wildlife Management* 33: 284–293.
- Newton, I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. *Biological Conservation* 70: 265–276.
- Nielsen, C.R., Parker, P.G. & Gates, R.J. 2006a. Intraspecific nest parasitism of cavity-nesting wood ducks: costs and benefits to hosts and parasites. *Animal Behaviour* 72: 917–926.
- Nielsen, C.R., Gates, R.J. & Parker, P.G. 2006b. Intraspecific ducks in natural cavities: comparisons with nest boxes. *Journal of Wildlife Management* 70: 835–843.
- Poff, B., Koestner, K.A., Neary, D.G. & Henderson, V. 2011. Threats to riparian ecosystems in Western North America: an analysis of existing literature. *Journal of the American Water Resources Association* 47: 1241–1254.
- R Development Core Team. 2014. *A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. Available on-line at <http://www.R-project.org> (last accessed 16 May 2016).
- Robb, J.R. & Bookhout, T.A. 1995. Factors influencing wood duck use of natural cavities. *Journal of Wildlife Management* 59: 372–383.
- Rohwer, F.C. & Freeman, S. 1989. The distribution of conspecific nest parasitism in birds. *Canadian Journal of Zoology* 67: 239–253.
- Ryan, D.C., Kawula, R.J. & Gates, R.J. 1998. Breeding biology of wood ducks using natural cavities in southern Illinois. *Journal of Wildlife Management* 62: 112–123.
- Semel, B. & Sherman, P.W. 1986. Dynamics of nest parasitism in wood ducks. *The Auk* 103: 813–816.

- Semel, B., Sherman, P.W. & Byers, S.M. 1988. Effects of brood parasitism and nest-box placement on wood duck breeding ecology. *The Condor* 90: 920–930.
- Semel, B. & Sherman, P.W. 1992. Use of clutch size to infer brood parasitism in wood ducks. *Journal of Wildlife Management* 56: 495–499.
- Semel, B. & Sherman, P.W. 1995. Alternative placement strategies for wood duck nest boxes. *Wildlife Society Bulletin* 23: 463–471.
- Semel, B. & Sherman, P.W. 2001. Intraspecific parasitism and nest-site competition in wood ducks. *Animal Behaviour* 61: 787–803.
- Strange, T.H., Cunningham, E.R. & Goertz, J.W. 1971. Use of nest boxes by wood ducks in Mississippi. *Journal of Wildlife Management* 35: 786–793.
- Yom-Tov, Y. 1980. Intraspecific nest parasitism in birds. *Biological Reviews* 55: 93–108.
- Yom-Tov, Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. *Ibis* 143: 133–143.



Photograph: A female Wood Duck flushes from a nest box as a technician gathers data, by Carl Taylor.