1 **An experimental test of information use by North American wood**

2 **ducks (*Aix sponsa*): external habitat cues, not social visual cues,**

3 **influence initial nest-site selection**

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19

Abstract

20

21 Birds may use a variety of cues to select a nest site, including external information on

22 habitat structure and nest site characteristics, or they may rely instead on social

23 information obtained directly or indirectly from the actions of conspecifics. We used an

24 experimental manipulation to determine the extent to which a California population of

25 the wood duck (*Aix sponsa*) used social information gleaned from visual cues inside

26 nest boxes that might indicate the quality or occupancy of that site. Over two nesting

27 seasons, we manipulated the contents of newly installed boxes to simulate one of three

28 states: (1) presence of wood duck eggs, indicating current use of a nest site; (2)

29 presence of down and shell membranes, indicating a previously successful nest; and (3)

30 control nests with fresh shavings indicating an unused box. In addition, we measured

31 habitat characteristics of the area surrounding each box to assess the use of external,

32 non-social information about each nest site. We found no evidence that females laid

33 eggs preferentially, or that conspecific brood parasitism was more likely to occur, in any

34 of the treatments. In contrast, nest site use and reproductive traits of wood ducks did

35 vary with vegetation cover, and orientation and distance of the box from water. Our

36 results suggest that personal information, not social information, influence initial nest

37 site selection decisions when females are unfamiliar with a site. Social cues likely

38 become increasingly important once nest sites develop their own history, and a

39 population becomes well established.

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Significance Statement

In selecting a nest site, birds may use many types of information, including habitat characteristics, their own previous breeding experience, or social cues inadvertently provided by other individuals of the same or different species. We examined information use in a Californian population of wood ducks by experimentally manipulating the visual cues within nest boxes and found that females did not use internal box cues to direct their nesting behaviors, appearing to rely on key habitat characteristics instead. These results contrast with previous studies of this system, suggesting that females may change the cues they use depending on their prior experience with a particular area. In the nest-site selection literature, there appears to be a divergence between research on passerines versus waterfowl, and we advocate unifying these perspectives.

Keywords: personal and social information use, waterfowl, *Aix sponsa*, nest-site selection, conspecific brood parasitism

Declarations

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Introduction

Animals use various types of information to make decisions about what to eat, where to live, and how to find mates or avoid predators. They can rely on "personal" information gleaned from the physical environment or from their own private experience (i.e., trial and error), or they can use "social" information, taking advantage of signals or cues provided by other individuals of the same or different species (Danchin et al. 2004). Social information can be based on 1) inadvertent cues about another individual's performance (typically referred to as "public" information), 2) the location of other individuals or 3) intentional signals produced by con- or heterospecifics (Danchin et al. 2004). This question of when and how animals use different kinds of information has inspired a growing number of theoretical studies and reviews (Bonnie and Earley 2007; Dall et al. 2005; Danchin et al. 2004; Dubois et al. 2012; Evans et al. 2016; Gil et al. 2019; Lee et al. 2016; Rieucau and Giraldeau 2011; Schmidt and Whelan 2010; Seppänen et al. 2007; Valone 2007), complemented by empirical studies exploring the impact of social information use on foraging behavior (Coolen et al. 2003; Machovsky-Capuska et al. 2014; Templeton and Giraldeau 1996), antipredator behavior (Frechette et al. 2014; Griffin 2004), mate choice (Nordell and Valone 1998), and breeding habitat selection (Danchin et al. 1998; Pöysä 2006; Vaclav et al. 2011). Evidence of social information use has been found in a wide array of taxa, including mammals (e.g., Ellard and Byers 2005; Lewanzik et al. 2019; Toelch et al. 2014), fish (e.g., Coolen et al. 2003; Elvidge et al. 2016; Webster and Laland 2017), amphibians and reptiles (e.g., Hobel and Christie 2016; Kar et al. 2017), insects (e.g., Avarguès-Weber et al. 2018; Grüter

118   and Leadbeater 2014), and birds (e.g., Aparicio et al. 2007; Roy et al. 2009; Tolvanen et

119   al. 2018).

120   The use of personal and social information has been especially well studied in

121   birds, particularly in the context of nest-site selection (Campobello and Sealy 2011;

122   Chalfoun and Schmidt 2012; Nocera and Betts 2010 and other contributors to a special

123   issue of *The Condor*; Szymkowiak 2013). In selecting a nest site, females may use

124   environmental cues such as food availability or habitat structure (Brown and Brown

125   1996; Orians and Wittenberger 1991) or nest site visibility (Bellrose and Holm 1994;

126   Semel and Sherman 1986; Semel and Sherman 1995; Semel et al. 1988).

127   Environmental cues are often more static or stable than social cues. Features of the

128   habitat (e.g., physical structure, vegetation, microclimate) are unlikely to change

129   markedly among breeding attempts and so may provide information that is reliable over

130   multiple years. However, because success likely depends on additional dynamics

131   operating at a local or population level (e.g., competition for nest sites, parasite loads,

132   predation risks), static environmental cues may not always provide reliable predictors of

133   success.

134   Alternatively, females may rely on information gleaned from other individuals. For

135   example, information on nest site preferences, use, and reproductive success could be

136   obtained by following or observing the actions of other conspecifics (Danchin et al.

137   1998; Pöysä 2006), heterospecifics (Mönkkönen and Forsman 2002; Parejo and Avilés

138   2007; Seppänen and Forsman 2007; Tolvanen et al. 2018), or both (Samplonius et al.

139   2017). These inadvertent socially-generated cues are frequently more ephemeral and

140   may operate on shorter timescales, within one or just a few breeding seasons. Social

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141   cues provide immediate information on nest site use or success by other birds, but that

142   information may not be reliable for future breeding attempts. Hence, while external

143   habitat cues and social cues both provide useful information – the time scale and

144   reliability of each source of information may vary. Moreover, the utility of either source of

145   information will also depend on the history of a given resource. A newly established nest

146   site, for example, would have little to no history and so nest site selection may be based

147   more on external habitat cues. Conversely, as nest sites develop their own history of

148   use and success, social cues might become more informative, albeit requiring on-going

149   re-assessment and refinement by the user. Accordingly, animals may use different

150   types of information at different points in the nest site selection process and as

151   information on the quality of a site accumulates over time.

152   One of the most commonly explored conspecific social cues is evidence of

153   current or past nest success (Boulinier et al. 2008; Danchin et al. 1998; Doligez et al.

154   2002; Kearns and Rodewald 2013; Kelly and Schmidt 2017; Parejo et al. 2008; Sergio

155   and Penteriani 2005; Ward 2005). For example, black-legged kittiwakes (*Rissa*

156   *tridactyla*) use the reproductive success of their neighbors to decide whether to

157   emigrate (Danchin et al. 1998); a more recent study of the same species showed that

158   individuals whose clutches failed were more likely to return to the same breeding habitat

159   the next year if their neighbors were successful (Boulinier et al. 2008). In collared

160   flycatchers *(Ficedula albicollis)*, immigration and emigration rates declined when

161   reproductive success was experimentally lowered (Doligez et al. 2002). Kearns and

162   Rodewald (2013) found that Northern cardinals (*Cardinalis cardinalis*), but not Acadian

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163   flycatchers (*Empidonax virescens*), adjusted the height and concealment of their nests

164   in response to both personal and social information about nest predation.

165   Curiously, two rather distinct research trajectories have developed among

166   researchers working on different groups of birds in their approach to investigating nest

167   site selection. In passerines, there has been a strong behavioral ecological orientation,

168   incorporating ideas on social information use and reliability into habitat selection models

169   (Ahlering et al. 2010; Ahlering and Faaborg 2006; Andrews et al. 2015; Nocera and

170   Betts 2010 and references above). Research on waterfowl and other gamebirds, in

171   contrast, has instead focused more on evaluating external habitat cues of resource

172   selection, specifically on the physical, environmental and resource variables birds may

173   be tracking to hone in on appropriate nesting locations (e.g., Clark and Shutler 1999;

174   Crabtree et al. 1989; Dyson et al. 2019; Gloutney and Clark 1997; Hines and Mitchell

175   1983 and see review by Eichholz and Elmberg 2014). One explanation for this is that

176   waterfowl studies have traditionally had a more applied management focus, with an

177   emphasis on identifying and protecting habitats that are particularly suitable for

178   waterfowl foraging and breeding. Classic wildlife studies, like those done on many

179   waterfowl species, have typically measured an array of relevant environmental variables

180   without necessarily incorporating information on social behavior (but see O'Neil et al.

181   2014; Pöysä et al. 1998). This is not to ignore the extensive literature on physical

182   habitat selection by passerines and other non-gamebirds (Jones 2001), but it is striking

183   that there has been a relative paucity of research on the use of social information in the

184   wildlife and waterfowl literature (Eichholz and Elmberg 2014; O'Neil et al. 2014; Pöysä

185   et al. 1998).

186   There is an exception to this trend, specifically for species that exhibit conspecific

187   brood parasitism (CBP), the laying of eggs in the nests of other females of the same

188   species. CBP occurs in a wide range of taxa, including insects, fish, and birds

189   (Andersson 1984; Brockmann 1993; Soler 2017; Yom-Tov 1980; Zink 2000), but is

190   particularly common among waterfowl (Eadie et al. 1988; Lyon and Eadie 2008;

191   MacWhirter 1989; Rohwer and Freeman 1989). CBP is unique in that parental and

192   parasitic tactics coexist in the same population. Curiously, this is one area in the

193   waterfowl literature where researchers have paid particular attention to the role of social

194   information, possibly because CBP is inherently a social interaction among females,

195   and the use of social cues over short time intervals may play an important role in how

196   parasites choose among possible host nests (reviewed in Pöysä et al. 2014). Studies of

197   social information use and CBP have been conducted on a number of waterfowl

198   species, including common goldeneyes (*Bucephala clangula*, Dow and Fredga 1985;

199   Pöysä 1999; Pöysä 2006), common eiders (*Somateria mollissima*, Fast et al. 2010;

200   Lusignan et al. 2010), red-breasted mergansers (*Mergus serrator*, Thimot et al. 2020),

201   and North American wood ducks (*Aix sponsa*, Odell and Eadie 2010; Roy et al. 2009;

202   Semel and Sherman 1986; Semel and Sherman 1995).

203   In the current study we attempt to bridge the gap between these two approaches

204   by investigating both external habitat (environmental) as well as social cues underlying

205   nest-site selection in a California population of the North American wood duck. Previous

206   research on this species suggests that females may rely on factors intrinsic to the site

207   itself, preferring nest boxes in highly visible areas (Bellrose and Holm 1994; Roy-

208   Nielsen et al. 2006; Semel and Sherman 1986; Semel and Sherman 1995; Semel et al.

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209 1988); but see (Jansen and Bollinger 1998). Separate studies have suggested that

210 females use social cues to assess the quality of individual nest-sites, laying

211 preferentially in previously successful nests (Hepp and Kennamer 1992); in nests that

212 were previously used but not necessarily successful (Roy et al. 2009); in active nests

213 containing eggs (Clawson et al. 1979; Wilson 1993); in active nests with low numbers of

214 eggs (Odell and Eadie 2010); or in nest boxes around which other ducks have gathered

215 (Heusmann et al. 1980; Semel and Sherman 1986; Semel and Sherman 1995; Wilson

216 1993). In wood ducks, the main cause of nest failure is nest desertion, not predation,

217 which might explain why females seem to be honing in less on previous nest success

218 compared to the highly depredated nests of common goldeneyes (Roy et al. 2009).

219   To tease apart which – if any - environmental and social cues females (nesting or

220 parasitic) may be using, we conducted an experimental field study in which we

221 manipulated the internal social cues in newly-erected nest boxes, while concurrently

222 collecting extensive habitat data at each nest site. We erected brand new boxes to

223 control for previous nest use and other historical factors that might influencing nesting

224 behavior (Pöysä et al. 2014). Wood ducks are particularly well-suited to this kind of

225 experimental study because they readily use nest boxes and exhibit generally high

226 levels of parasitic behavior. Over the course of two field seasons, we experimentally

227 manipulated nest contents to mimic one of three different conditions: an unused nest

228 (control, with wood shavings); an active nest during the laying stage (with eggs sitting

229 on top of the shavings); or a previously successful nest (with eggshells and down). This

230 allowed us to test whether females are using evidence of previous/current box use to

231 direct their laying strategies, and whether these tactics differ among nesting versus

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232   parasitic females. At each nest box site, we also collected data on an array of

233   environmental variables, including box visibility and orientation, proximity to water, and

234   distance between boxes.

235   If females are preferentially selecting previously successful nest sites (i.e., "safe"

236   sites with lower predation risk, Pöysä 1999; Pöysä 2006), then we would expect them to

237   favor the nests with down and eggshells in them. If they are using current box use as a

238   guide (Clawson et al. 1979; Odell and Eadie 2010; Wilson 1993), then boxes with eggs

239   already in them should be favored – particularly by parasitic (non-incubating) females.

240   Conversely, if females avoid nests with evidence of current occupancy, treatment boxes

241   with eggs should be avoided. Alternatively, it is possible that females pay little or no

242   attention to internal box cues, relying instead on key habitat characteristics that might

243   provide more reliable long-term (static) information – at least for "new" nest sites such

244   as these. A final possibility is that females are using some combination of personal and

245   social information.

246

247   **Methods**

248   *Study Area*

249   Our study was conducted within the Putah Creek Reserve in Davis, California during

250   March-July of 1998 and 1999. New nest boxes were erected along lower Putah Creek,

251   located at the southern end of the Putah-Cache Creek watershed. This natural

252   waterway winds through both urban and agricultural landscapes and is an important

253   resource for both farmers and wildlife. Our study site was divided into two sections, 1)

254   "Putah Creek" (PC), a 5.52 km (63.2 ha) section of the creek where a total of 37 boxes

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255   were erected 41-469 m apart (mean = 157 m; 0.62 boxes/ha), and 2) "Russell Ranch"

256   (RR), a 1.79 km stretch (24.75 ha) located approximately 6 km downstream from PC

257   where we erected 12 boxes at similar density, one box every 87-207 m (mean = 130 m,

258   0.93 boxes/ha). Along PC, 34 of the 37 boxes were erected just prior to the 1998

259   nesting season; 4 were erected in 1997 after the nesting season but were not set up for

260   use until 1998. At RR, 7 of the boxes were erected in 1997 and 5 were erected at the

261   end of the nesting season in 1998, but none of the boxes were set up for use until just

262   prior to the 1999 nesting season. Nest box density at both sites was far lower than that

263   reported in many other studies of wood ducks (e.g., Semel and Sherman 1995), and

264   closely approximated natural cavity densities – e.g., 0.68 cavities/ha (Soulliere 1988),

265   4.0 cavities/ha, range 0.8–15.3 cavities/ha (Gilmer et al. 1978). Boxes were placed

266   between 1.5 and 5 m (mean = 3 m) above the ground primarily on oak (*Quercus*),

267   cottonwood (*Populus*), walnut (*Juglans*), and eucalpytus (*Eucalyptus*) trees located

268   between 2 and 60 m (mean = 16 m) from the bank of the creek.

269

270   *Experimental Manipulation of Internal Box Environment*

271   The visual cues influencing female nest-site selection were analyzed experimentally

272   using the responses of females to various nesting conditions, simulated by different

273   combinations of wood duck eggs, down, and eggshells. The responses of breeding

274   females to nests with eggs in them (representing active or recently abandoned nests),

275   nests with down and eggshells in them (representing either successfully hatched or

276   predated nests), and empty (unused) nests was recorded to see which nest-site

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277   conditions most attract females. During each breeding season, we randomly assigned

278   each nest box to equal numbers of the three treatments, defined as follows:

279   1. Control: Our control treatment consisted of a 10-cm layer of wood shavings. This is

280   the standard way of prepping a nest box for use by wood duck females.

281   2. Eggs: To simulate an active or recently abandoned nest, we placed three eggs on

282   top of approximately 10 cm of wood shavings. We used either unhatched wood

283   duck eggs, wood duck eggs from a recently-abandoned nest, or when no fresh duck

284   eggs were available, unfertilized chicken eggs. Chicken eggs are similar in color,

285   size, and shape to wood duck eggs and thus closely approximated natural

286   conditions.

287   3. Down and eggshells: Nesting wood ducks produce a layer of down with which they

288   cover eggs during forays off the nest. When eggs hatch, pieces of shell and

289   membranes are consistently left behind with the down. To simulate a successfully

290   hatched nest, we placed a 3-cm layer of wood duck down interspersed with

291   eggshell membranes and shell fragments onto wood shavings. The down and

292   membranes were collected from old nests that had either produced ducklings or

293   were predated after hatch.

294   In 1998, we worked only at the PC site and conducted one set of experiments,

295   establishing treatment nests in newly-erected nest boxes between March 15 and April

296   24. In 1999, we included 12 boxes at the RR site and conducted two sets of replicate

297   experiments at each site. From March 3 to March 17 before nesting began, we

298   randomly assigned each nest box to equal numbers of the three treatments. From May

299   5 to May 24 we repeated the experiment and reset all boxes that had not been used

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300   and re-randomized treatments. We realize that females might have responded

301   differently to boxes depending on their familiarity with them. For this reason, we

302   conducted different analyses depending on each of these sets of treatments, as

303   described in "Statistical Analyses" below.

304

305   *Nest Monitoring and Identity of Reproductive Tactics*

306   Nest checks every other day as well as close monitoring of females determined which

307   nest boxes were being selected by which females and whether or not the eggs laid in

308   these boxes were subsequently incubated. During each nest check, the box was

309   plugged to prevent the female, if present, from flushing from the nest. This minimized

310   the danger of egg damage and allowed us to identify (and individually mark, if we had

311   not already done so) the nesting female. We recorded the following nest stages:

312   'playing house,' (the wood shavings were disturbed, or there was a depression in the

313   shavings, but no eggs were present) 'laying,' (one or more eggs were present but were

314   at ambient temperature), and 'incubation' (if a female was present and eggs were warm,

315   or if a female was absent but eggs were warm and covered with down). In active nests,

316   we used a fine-tipped permanent marker to number the end of each egg.

317   We established the possible presence of parasitic females using a combination

318   of techniques, including nest-trapping and banding of females and regular monitoring of

319   all active nests. A nest was considered parasitized if any of three criteria were met:

320   more than one egg was laid per day, the total number of eggs in a clutch exceeded 13,

321   or eggs were laid after the onset of incubation (Eadie et al. 2010). These criteria are

322   well-established proxies for nest parasitism (Brown 1984; Eadie et al. 2010; Gibbons

323   1986; Lyon and Eadie 2017; Yom-Tov 1980).

324

325   *External Environmental Characteristics*

326   To examine the alternative hypothesis that females select and use nest sites based on

327   external environmental characteristics instead of, or in addition to, internal box cues, we

328   collected data on an extensive series of habitat features, incorporating 20 variables

329   related to: (i) vegetation cover at the nest site, (ii) tree species and stand composition,

330   (iii) proximity to other trees, nest boxes or water, (iv) orientation and height of the box,

331   and (v) characteristics of the shoreline. These variables are summarized in Table 1 with

332   abbreviations referred to in analyses.

333   We attempted to establish identical sets of experimental nest boxes strategically

334   placed in two different habitat types, an "open" habitat in which the nest boxes are

335   highly visible, and a "closed" habitat in which the boxes are well obscured by vegetation.

336   This distinction between habitat types is useful because it can help determine whether

337   females are basing their selection of nest site and their subsequent laying strategy

338   solely on the quality of nest boxes they encounter, on their location, or on both. Some

339   nests were occupied by other wildlife and some of the experimental treatments were

340   disturbed (e.g. eggs broken in nest) so that sample sizes varied slightly among

341   treatment and years.

342

343 *Statistical Analyses*

344 Our analyses were dependent on which sets of boxes were included. Some boxes were

345 used by other wildlife and so became unavailable (Table 2). We excluded those nests

346 from all analyses. Further, because we used the same nest boxes erected in 1998 for

347 experiments in 1999, a small number of boxes that were used in 1998 had previous

348 history, creating heterogeneity in our sample. In our final analysis we excluded those

349 nest boxes from the 1999 sample, using only the data from the first nests in 1998. Some

350 nest sites were also used more than once by wood ducks in a given year. Again, to

351 ensure that birds were responding only to our experimental treatment and not to

352 additional information from the current nesting season, we analyzed only the first

353 attempts for each box. Our goal was to ensure that, at the start of each experiment,

354 every box had no prior history. Finally, our second replicate set of experiments in May

355 1999 yielded few additional nests and most boxes were unused (due to the time of the

356 season). We therefore excluded the second replicate because it confounds the time of

357 season when the treatments were initiated and simply adds large numbers of unused

358 boxes that dominate the sample. Our very conservative approach has the limitation that

359 it reduces sample size, but it ensures that we are evaluating the response of birds to the

360 same sets of cues. Where appropriate, we note the patterns found when we relax our

361 criteria; the results remained unchanged.

362   We used generalized linear models (GLMs) throughout (JMP 2018). Our first set

363 of analyses focused on nest use as influenced by our experimental treatments; given

364 strong year effects we include both treatment and year in all models. We examined

365 several response variables; we first considered Use/No Use of the nest box as indicated

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366   by the presence of eggs and/or an incubating female. For sites that were used, we then

367   examined the Number of Eggs Laid, Number of Eggs Hatching, and Date First Egg laid

368   (Julian). Use/No Use was a binomial response variable, and we examined the effects of

369   the experimental treatments using a GLM with a binomial distribution and logit link

370   function. Number of Eggs Laid, Number of Eggs Hatched, and Date of First Egg Laid

371   were treated as count data, and we examined the effects of the experimental treatments

372   using a GLM with a Poisson distribution and a log link function. GLMs and Poisson

373   models are prone to overdispersion and without correcting can give erroneous results

374   (JMP 2018). Accordingly, for each analysis we included an overdispersion correction

375   parameter (Pearson Chi-square deviance divided by the degrees of freedom (DF) for

376   the full sample in the model). With overdispersion, a correction will be more robust and

377   possibly more conservative. We employed the Firth bias-adjusted method to fit the

378   model (Firth 1993).

379   Our second set of analyses examined a number of external habitat and nest

380   characteristics that might provide an alternative source of information for breeding

381   females. We initially considered 20 external habitat and nest variables (Table 1). A

382   principal components analysis did not help to reduce these to a simple interpretable set

383   of habitat dimensions, and so we retained the original variables. As in the first set of

384   analyses, we examined several response variables, first considering Use/No Use of the

385   nest site; for sites that were used, we then examined the effect of habitat characteristics

386   on the Number of Eggs Laid, Number of Eggs Hatching, and Date First Egg laid

387   (Julian). To explore the potential influence of these variables, we initially conducted

388   simple bivariate analysis to identify a smaller subset of external characteristics that

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389   might influence each response variable, and we conducted exploratory stepwise

390   selection methods (forward selection using minimum AICc as guiding rule). From these

391   analyses, we focused on the subset of habitat variables that appeared to have some

392   influence on each response variable. We conducted GLMs as described above, fitting

393   multiple models with different combinations of habitat variables. We also contrasted

394   each model with a similar model that included experimental treatment as an additional

395   factor. Although many of these models were highly significant in a statistical sense (P-

396   values << 0.01) we instead ranked models used a model selection approach based on

397   minimum values of AIC_c (Akaike Information Criterion corrected for small sample size;

398   Burnham and Anderson 2002). We emphasize that the goal of these analyses was *not*

399   to fit a predictive model, nor even to determine which habitat variables might be best

400   predictive of wood duck nest use. Rather, we were most interested in determining: (1)

401   whether any subset of external variables had utility in evaluating wood duck use (do

402   external cues matter?) and more importantly, (2) whether internal nest cue treatments

403   provided additional or better explanatory power.

404

405   **Results**

406   A total of 34 treatments was established in 1998, and 47 treatments in 1999 (Table 2).

407   However, eight boxes in 1999 had been used by wood ducks in the previous year or in

408   a previous attempt in 1999 and were thus excluded from the final analysis. The second

409   replicate set of treatments in boxes in late May 1999 (N = 32) was also excluded to

410   avoid confounding date and lack of use late in the season (see Methods). Sample sizes

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411   differed slightly between years and treatments due to use or interference by other

412   wildlife (Table 2).

413   Manipulation of the internal box environment through the experimental addition of

414   either eggs, egg shells and down, or wood shavings had little effect on box use by wood

415   duck females. Over the 1998 and 1999 breeding seasons, females nested in 20 of the

416   81 boxes that were included in the experiment (Table 2). After excluding boxes used

417   previously by wood ducks and those used by other wildlife, 56 Treatment boxes were

418   available for analysis (22 Control, 17 Down, 17 Egg treatments). We found no effect of

419   Treatment on Nest Box Use (Likelihood ratio X^2 = 2.75, P = 0.25; Table 3). Contrary to

420   our predictions, there was a trend for Control boxes to be used more (50%) compared

421   to either Down (29%) or Egg treatments (24%; Figure 1). This pattern did not change

422   when we relaxed our criteria and included boxes that had been previously used (Control

423   50% of 24 boxes used, Down 38% of 21 boxes used, and Egg 32% of 19 boxes used).

424   Year had a strong influence on Nest Box Use (Likelihood ratio X^2 = 9.95, P = 0.002;

425   Table 3), largely because nest box use was low in 1998 compared to 1999 (Table 2).

426   We also found no influence of treatment on Number of Eggs Laid or Julian Date

427   of First Egg (Table 3) although there was a significant effect of treatment on the Number

428   of Eggs Hatching (Likelihood ratio X^2 = 6.17, P = 0.05; Table 3). Fewer eggs hatched in

429   the Egg treatment (Figure 2). The Julian date of First Egg was influenced by year;

430   nesting was considerably earlier in 1999.

431   Our analysis of a comprehensive set of external habitat cues suggest that a small

432   number of characteristics influence nest use and reproductive success of wood ducks

433   (Table 4). Notably, nest box Use was influenced by nest box visibility, presence of trees

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434   in front of the box, and orientation. Both the Number of Eggs Laid and the Number of

435   Eggs Hatching were influenced by the direction and distance to water (Table 4). Several

436   of these patterns were highly significant ($P< 0.01$), indicating that external habitat

437   characteristics influence nest site use and investment in newly erected nest boxes.

438   A central question for our study was how wood ducks might make use of two

439   different kinds of information: external habitat cues versus social cues. To fully contrast

440   these alternatives, we considered the habitat models identified above (Table 4) and ran

441   the models with the same subset of habitat variables but also including the effects of

442   experimental treatment to allow both sets of 'cues' to compete for the data. These

443   analyses further suggest that wood ducks do not make use of social cues but instead

444   rely on a few habitat characteristics. For three of the four reproductive measures

445   considered, only habitat variables were included in the top models ($\Delta Aic_c > 3$ or greater,

446   Table 4). The one exception was for the Number of Eggs Laid, for which inclusion of

447   treatment effects in addition to direction to water comprised the top model ($\Delta Aic_c = 7.4$,

448   Table 4).

449   Finally, we found no evidence that any of the treatment nests were more likely to be

450   parasitized. Considering all treatment nests (including those previously used) there was

451   evidence of only 6 nests being parasitized as indicated by observations of > 1 female on

452   the nest, clutch size sizes >13 eggs, or eggs laid after incubation. Of these, 2

453   parasitized nests occurred in each treatment.

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Discussion

Over the course of our two-year field experiment, we found no evidence that wood duck

females used social cues about the internal state of the nest box at the beginning of the

breeding season, at least not when boxes were brand new to an area. This result was

somewhat surprising given that a recent study of long-term patterns of nest use by

wood ducks on our study area (including Putah Creek although not during the years of

the current study) found that females were more likely to use nest sites that had been

previously used by other females (Roy et al. 2009). Other studies likewise suggest that

wood ducks use social cues to assess the quality of individual nest-sites, such as

evidence of previous success (Hepp and Kennamer 1992); nests containing eggs

(Clawson et al. 1979; Odell and Eadie 2010; Wilson 1993); or nest boxes around which

other ducks have gathered (Heusmann et al. 1980; Semel and Sherman 1986; Semel

and Sherman 1995; Wilson 1993). In our previous study (Roy et al. 2009), we found no

evidence that previous success influenced future nest box use, and so we hypothesized

that females were cueing in to activities or signs of use by other females. If this were the

case, and females were using internal box cues rather than actual knowledge of box

use to guide their decisions, there should have been no difference in box use between

egg treatments (representing active nest) and shells-and-down treatments (representing

a previously successful nest), but significantly more use of those two treatments

combined than of unused boxes (those with wood shavings only). In fact, although we

did find that females were just as likely to use boxes with eggs and shells-and-down, if

anything they showed a slight preference for empty "unused" nests with just shavings

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479 inside. Our results suggest that internal cues do not attract females to a nest-site and

480 may even cause females to avoid these sites.

481   Although females were not using social cues about previous or current box use

482 to choose a nest-site, they did seem to be paying attention to specific habitat

483 characteristics. They were significantly more likely to nest in boxes that were located in

484 more open visible locations, with few trees in front of the entrance and oriented towards

485 and closer to water (Table 4). None of these patterns are unexpected and suggest that,

486 for the females in our experiment at least, simply finding a nest site may be the central

487 challenge and external habitat features might be most influential.

488   In stark contrast to our study, evidence for social information use has been

489 documented in a number of other waterfowl species, particularly in the context of

490 conspecific brood parasitism. For example, in cavity-nesting common goldeneyes,

491 parasitic females appear to be using predation risk as a cue, preferentially selecting

492 nest boxes that have not been depredated the previous year (Pöysä 1999; Pöysä 2006;

493 Pöysä et al. 2010; Pöysä and Paasivaara 2015). In contrast, a study of red-breasted

494 mergansers in Canada (Thimot et al. 2020) found that females were not preferentially

495 selecting "safe" nest sites, likely because egg predation rates were low in this

496 population. Rather, the presence of conspecifics seemed to be a cue: artificial nests

497 with no host attracted fewer brood parasites (Thimot et al. 2020). Among common

498 eiders, also a ground-nester, nest visibility impacts parasitism rates more than nest site

499 safety (Lusignan et al. 2010). Another experimental study of eiders examined the

500 specific cues females might use, indicating that they are more likely to lay in nests that

501 had nest materials (down) in them – indicating previous nest success (Fast et al. 2010).

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502 Finally, mallards (*Anas platyrhynchos*, Pöysä et al. 1998) and lesser scaup (*Aythya*

503 *affinis*, O'Neil et al. 2014) apparently use social cues such as conspecific density and

504 proximity to previously successful nesting habitats in selection of breeding and nesting

505 sites.

506   The question thus remains: why didn't wood ducks in our study use social cues

507 to guide their nesting choices, despite evidence from other years, populations and

508 species suggesting that such social cues may be informative? We suggest several

509 possibilities. *First, it may be that our experimental design and/or sample sizes were*

510 *insufficient to detect patterns that might exist*. Although we erected a large number of

511 nest boxes and established 81 possible treatment nests over two years, the final sample

512 size was dictated by how the birds responded. As expected, there was little use in the

513 first year but considerably more in the second (accounting for the strong year effect in

514 nest box use; Table 3). Moreover, by using brand new boxes, our goal was to eliminate

515 any previous history associated with each box and so, by design, we knew it would take

516 time for birds to discover and use our nest boxes. Indeed, it was this very process of

517 initial nest site selection that we wished to explore to determine how external habitat

518 cues relative to internal visual social cues might influence nest site selection decisions

519 by new females. Further, we used very conservative criteria for inclusion in our

520 analyses, removing any site that was used in the first year (even though it was a new

521 box that year) from analysis in the second year to ensure that previous history would not

522 confound our analyses. Nonetheless, even when we relaxed these strict criteria, the

523 same patterns remained – females did not disproportionately use nests with evidence of

524 prior use. In fact, if anything, the trend was in the opposite direction regardless of which

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525   boxes were included – control boxes were more likely to be used, albeit not significantly

526   (Figure 1), and huge sample sizes and a strong shift in patterns of nest site use would

527   be required to alter the results. Finally, despite the more restricted samples sizes when

528   we applied our conservative criteria, we were still able to detect statistically significant

529   differences when considering habitat variables (Table 4). We conclude that

530   experimental design or restricted sample sizes cannot account for the lack of use of

531   visual social cues by wood ducks in our study; the patterns appear to be robust.

532   *A second possibility is that internal box cues simply are not used by these wood*

533   *ducks to assess nest quality, at least during a female's first nest attempt of the season.*

534   If cavities are a rare commodity in nature, simply finding a nest that is usable may be

535   the top priority. Alternatively, the lack of attention to internal cues may have more to do

536   with when and how females prospect for nests. Common goldeneyes, which do appear

537   to use box cues (Pöysä 2006), prospect for nests at the end of the breeding season

538   (Eadie and Gauthier 1985; Eadie et al. 1995), when evidence of recent nesting activity

539   is presumably still fresh. In contrast, wood ducks prospect for nests in the spring

540   (Bellrose and Holm 1994; Dixon 1924; Hepp and Bellrose 1995). If the timing of nest

541   searching is key, and given that wood duck females do not regularly encounter

542   evidence of previous nesting activity in the spring, selection might not have acted on

543   females to recognize or respond to internal box cues. Also, female wood ducks in

544   general may be less selective than goldeneyes in part because of the relatively low

545   rates of nest predation in wood ducks (discussed in Roy et al. 2009), and/or the speed

546   with which wood ducks reach reproductive maturity. Female wood ducks reproduce at

547   one year of age (Bellrose and Holm 1994), whereas goldeneyes exhibit deferred

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548   maturity and typically do not breed until they are two years of age or older, increasing

549   the opportunity for nest exploration and information use (Eadie and Gauthier 1985;

550   Eadie et al. 1995). However, this would not explain why other populations of wood

551   ducks (Clawson et al. 1979; Hepp and Kennamer 1992; Wilson 1993), and even the

552   same population of wood ducks (Odell and Eadie 2010; Roy et al. 2009) do seem to be

553   paying attention to box cues such as the presence of eggs or down.

554   *A third possibility is that female wood ducks do rely on social cues, but pay more*

555   *attention to the presence or activity of other wood duck females.* Betts et al. (2008) refer

556   to such cues as 'location cues' indicated by the presence or position of other individuals,

557   in contrast to 'public information' indicated by the success or performance of other

558   individuals at the site (Danchin et al. 2004; Valone 1989). For example, a number of

559   studies of other wood duck populations have suggested that females may be using cues

560   such as the presence of females at the nest (Heusmann et al. 1980; Semel and

561   Sherman 1986; Semel and Sherman 1995; Wilson 1993). When Wilson (1993) placed

562   decoys of females near nest boxes, brood parasitism rates at those nests increased.

563   This decoy effect has also been found in a number of other non-waterfowl bird species.

564   For example, in obligate brood parasitic species such as cuckoos, simply placing

565   experimental parasitic eggs in host nests did not elicit the maximum response by the

566   host; the presence of cuckoo females nearby or at the nest (or a taxidermic mount)

567   significantly increased rejection rates of experimental eggs (Davies and Brooke 1988;

568   Langmore et al. 2009; Moksnes et al. 1993). This suggests that physical cues such as

569   the presence of eggs alone may be insufficient to elicit a behavioral response; it may

570   not be evidence of use, but rather visual confirmation of active use that matters. More

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571 recent data for our population of wood ducks also points to the strong influence of social

572 information use and conspecific activity. For the past six years we have used Passive

573 Integrated Transponders (PIT tags) and radio frequency identification detection (RFID)

574 readers on every nest box on over 200 boxes at four study sites and we have PIT-

575 tagged over 500 females. These data have revealed surprising and remarkable

576 evidence that females prospect for nests in groups, visit a large number of nest sites

577 before breeding, and that different sites – even close by – attract very different numbers

578 of females, suggesting that conspecific cueing and information use may yet play a

579 significant role in nest site selection processes by wood ducks (JME and colleagues,

580 unpublished data).

581 *A final intriguing possibility is that females use different kinds of information,*

582 *including both social and environmental cues, but their relative use of these cues varies*

583 *over space and time and may be sequentially applied.* Our specific findings (use of

584 habitat cues, not internal box cues) could be explained by the fact that our nest boxes

585 were new. In the absence of information on past history of the boxes, females might

586 instead utilize external habitat characteristics as the best initial estimate of the quality of

587 the nest site. The challenge for a newly breeding female is simply to find a relatively

588 rare but suitable nest site, and habitat cues would be available and perhaps more

589 predictable than social cues. A shift to reliance on social cues may come only after

590 more information about a site is acquired and the site has developed its own history of

591 use and success. External habitat cues, over time, may not adequately predict local

592 dynamics such as the influence of local densities of competitors (conspecifics and other

593 species), predators, or the buildup of ectoparasite loads of lice, fleas, or mites in a nest

594   box. At a new breeding site, such as the ones we established in 1998-1999, females

595   may first need to gain familiarity with the "real estate" in the neighborhood, before

596   shifting their attention to the activities and success of their neighbors. As nest sites

597   develop a history, more refined assessments of nest site quality are possible, and it is

598   here when social cues may be most useful. Thus, it is not so much a question of *do*

599   birds use *either* external personal (habitat cues) *or* social information cues, as often

600   posed, but rather *when* and under what circumstances might either or both types of

601   cues be useful. This could also account for the observation that different studies, even

602   on the same species such as wood ducks, yield different results regarding information

603   use (see above). With over 20 years of data on this population, and six years of PIT tag

604   and RFID data, we should be able to address this possible shift in focus in future

605   studies.

606   We also found no evidence that parasitic and parental females differed in box

607   use, although the frequency of parasitism was low during the two years of our study.

608   This again may be a consequence of the early stage of our study, such that local

609   populations had not yet increased and competition for nest sites was low; conspecific

610   parasitism may be less frequent under these conditions (see Semel and Sherman 1986;

611   Semel and Sherman 1995; Semel et al. 1988). There is evidence that CBP in wood

612   ducks is density-dependent (Clawson et al. 1979; Heusmann et al. 1980; Semel and

613   Sherman 1986) and so it would not be unexpected that parasitic females might rely

614   more on the use of social cues to select host nests in larger established populations as

615   found in common goldeneyes (Dow and Fredga 1985; Pöysä 1999; Pöysä 2006),

616   common eiders (Fast et al. 2010; Lusignan et al. 2010), and red-breasted mergansers

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617   (Thimot et al. 2020). Interestingly, the only effect of our experimental treatments, when

618   habitat features were controlled, was on the number of eggs laid and a trend towards

619   fewer eggs hatching (Table 4, Figure 2). Perhaps nests with eggs attracted parasitic

620   females to lay a few eggs in those nests, and nests closer and more directly facing the

621   water might be more accessible. In any case, we did find that wood ducks readily used

622   nest sites already containing eggs, suggesting that they do not avoid sites even where

623   there is evidence of current occupancy. Odell and Eadie (2010) found a similar pattern

624   in a separate experiment with wood ducks, suggesting that abandoned eggs could

625   subsequently be included in a clutch of a new female who then incubates the nest.

626   Whether this represents accidental "parasitism' or more covertly, a form of "pre-emptive

627   parasitism" is an intriguing question and may be a factor contributing to the high

628   frequency of conspecific brood parasitism observed in this species.

629   Our results have management and conservation implications and offer some

630   insight on the divergent trajectories that appear to characterize nest site selection

631   studies by gamebird vs. non-gamebird bird ecologists. A large number of studies have

632   now recognized the importance of both social and personal information use in nest site

633   selection by birds (Ahlering et al. 2010; Ahlering and Faaborg 2006; Betts et al. 2008;

634   Campobello and Sealy 2011; Chalfoun and Schmidt 2012; Coulton et al. 2011; Nocera

635   and Betts 2010; Szymkowiak 2013; Ward et al. 2010). However, studies of waterfowl

636   have focused more on habitat characteristics affecting nesting behaviors, while studies

637   of passerines tend to focus more on the importance of social information (see also

638   Eichholz and Elmberg 2014; O'Neil et al. 2014). Until now, the data on waterfowl have

639   not been deeply integrated into the broader literature on public information use in other

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640   birds, but we advocate that both research realms would benefit by more cross-

641   pollination (see O'Neil et al. 2014 for a similar perspective). The way different species

642   and populations balance the use of personal versus social information undoubtedly

643   varies, not only among species (the focus of much current literature), but also over

644   different temporal and spatial scales. We suggest that the temporal scale of information

645   use, in particular, has not been widely investigated – the types of cues used for initial

646   nest site discovery might be very different from those used to refine or adjust nest

647   selection decisions. Perhaps even more importantly, in light of both rapidly changing

648   climates and habitats, and huge investments in habitat conservation, the pace at which

649   each type of information varies could be critical (e.g., habitat structure is likely to change

650   gradually whereas social cues related to reproductive success or performance could

651   change drastically within a single nesting season; Betts et al. 2008). Wildlife biologists

652   working to create or restore high quality nest site habitat may experience limited

653   success if social cues are more important in the early stages of nest site discovery and

654   attraction (Ahlering et al. 2010; Ahlering and Faaborg 2006; Nocera and Betts 2010;

655   Ward et al. 2010). Conversely, providing evidence of social cues to attract birds to new

656   habitats when the underlying habitat conditions are inadequate or deteriorating could

657   attract birds into an ecological trap (Schlaepfer et al. 2002) unless birds use external

658   habitat cues to avoid those locations initially. A deeper understanding of how multiple

659   cues and sources of information are integrated throughout an individual's lifetime and at

660   critical life history junctures may have valuable conservation applications.

661

662 **Table 1** List of habitat variables measured at each nest box for experimental nests

Abbreviation	Description
Height	Nest box height (m)
Dist Nest Box	Distance to nearest nest box (m)
Comp Dir	Compass orientation of entrance (°)
Dir Water	Compass orientation toward water from box entrance (°)
Dist Water	Distance to water from box entrance (m)
% Cov Grd	% Vegetation cover at ground - base of nest (0-100%)
% Cov E	% Vegetation cover at entrance level of nest (0-100%)
% Cov 5m	% Vegetation cover at 5 m height above nest (0-100%)
Canopy HT	Estimated height of top of tree canopy at box location
% VIS	Estimated % visibility of nest entrance (0-100%)
Tree Species	Tree species on which box was mounted: eucalyptus (EUCA), valley oak (QULO), Fremont cottonwood (POFE), California black walnut (JUCA), willow (SALX)
Std Type	Stand type – predominant tree species of stand where box mounted
Std Size	Stand size – ordinal ranking from 1 (small; 1-5 trees) to 4 (continuous)

Std Density	Stand density – ordinal ranking from 1 (sparse,1 tree/20m) to 4 (dense; 1 tree/5m)
Tree 0m	Distance to nearest tree in front of box (0°)
Tree 90m	Distance to nearest tree to right of box (90°)
Tree 180m	Distance to nearest tree behind box (180°)
Tree 270m	Distance to nearest tree to left of box (270°)
SLP	Estimated slope from box to nearest water (°)
% Shcov	% vegetation cover along shore of nearest water
TREAT	Experimental treatment (control, down, eggs)

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666 **Table 2** Sample sizes of experimental nests in each year. A number of nests were

667 used by other wildlife and so were excluded from analysis. Additionally, some boxes in

668 1999 had been used in the previous year by wood ducks (numbers in parentheses) and

669 so were also excluded from final analysis

Treatment	Number Available	Used by Wood Ducks	Not Used by Wood Ducks	Used by Other Wildlife
1998				
Control	12	1	9	2
Down	11	3	8	0
Eggs	11	1	8	2
Total	**34**	**5**	**25**	**4**
1999				
Control	15 (2)	10 (1)	2 (1)	3
Down	11 (4)	2 (3)	4 (1)	5
Eggs	13 (2)	3 (2)	5 (0)	5
Total	**39 (8)**	**15 (6)**	**11 (2)**	**12**
Both Years				
Control	27 (2)	11 (1)	11 (1)	5
Down	22 (4)	5 (3)	12 (1)	5
Eggs	24 (2)	4 (2)	13 (0)	7
Total	**73 (8)**	**20 (6)**	**36 (2)**	**17**

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670 **Table 3** Generalized Linear Models (GLM) to examine the influence of nest box

671 treatment (control, down added, eggs added) and year (1998, 1999) on nest box use,

672 number of eggs laid, number of eggs hatching, and date of first egg laid for wood ducks

673 near Davis CA. Analyses were conducted for only the first nest attempts at each box

674 each year

Model	N	- LLH [a]	LR Chi Sq [b]	DF [c]	P [d]	OD [e]
1. **Use** [f]						
Whole Model	56	6.63	13.27	3	0.004	1.00
Treatment			2.75	2	0.25	
Year			9.95	1	0.02	
2. **Number of Eggs Laid** [g]						
Whole Model	20	1.57	3.15	3	0.37	0.56
Treatment			0.94	2	0.61	
Year			2.50	1	0.11	
3. **Number of Eggs Hatching** [g]						
Whole Model	20	3.11	6.22	3	0.10	1.17
Treatment			6.17	2	0.05	
Year			0.01	1	0.99	
4. **Julian Date of First Egg** [g]						
Whole Model	20	10.79	21.58	3	0.0001	3.34
Treatment			0.02	2	0.99	
Year			4.38	1	<0.0001	

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676   [a] –Log likelihood; difference of the log likelihoods of the full and reduced (intercept only) models

677   [b] Likelihood ratio Chi square

678   [c] Degrees of Freedom

679   [d] P value for Likelihood Chi square

680   [e] Overdispersion parameter (Pearson Chi square deviance / degrees of freedom of goodness of

681   fit test)

682   [f] Generalized Linear Model, Binomial distribution, Logit link function, corrected for

683   overdispersion

684   [g] Generalized Linear Model, Poisson distribution, Log link function, corrected for overdispersion

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687 **Table 4** Generalized Linear Models (GLM) to examine the influence of Habitat

688 Variables and Treatment on nest box use, number of eggs laid, number of eggs

689 hatching, and date of first egg laid for wood ducks near Davis CA. Data for both years

690 are included in analyses. Models are ranked using AIC_c Akaike Information Criterion.

691 Habitat variable abbreviation and description are in Table 1. TREAT: experimental nest

692 treatment (control, eggs, down)

Model	N	- LLH [a]	LR Chi Sq [b]	DF [c]	P [d]	AIC_c [e]	OD [f]
1. **Use** [g]							
Tree 0m, % Vis	52	5.79	11.59	2	0.003	64.35	1.00
Tree 0m, % Vis, Comp Dir	52	6.54	13.09	3	0.004	65.30	1.00
Tree 0m, % Vis, Comp Dir, Dist Water	52	6.92	13.85	4	0.008	67.11	1.00
Tree 0m, % Vis, TREAT	52	6.45	12.91	4	0.012	68.05	1.00
Tree 0m, % Vis, Comp Dir, TREAT	52	7.26	14.53	5	0.013	69.10	1.00
Tree 0m, % Vis, Comp Dir, Dist Water, TREAT	52	7.44	14.88	6	0.021	71.56	1.00
2. **Number of Eggs Laid** [h]							
Dir Water, TREAT	20	5.96	11.91	4	0.018	247.48	0.39
Dir Water	20	5.79	11.58	2	0.003	254.89	0.37
Dist Water, Dir Water	20	13.43	26.85	3	0.0001	365.33	0.25
Dist Water, Dir Water, TREAT	20	17.59	35.18	3	0.0001	420.96	0.22

3. Number of Eggs Hatching [h]

Std Type	20	3.37	6.74	3	0.08	98.60	1.22
Dir Water	20	1.05	2.10	2	0.35	98.91	0.35
Dir Water, TREAT	20	3.92	7.84	4	0.097	102.11	1.21
Dir Water, Std Type	20	4.95	9.90	5	0.08	106.65	1.19
Std Type, TREAT	20	7.83	15.66	5	0.008	120.81	0.98
Dir Water, Std Type, TREAT	20	11.97	23.94	7	0.0012	139.12	0.87

4. Julian Date of First Egg [h]

SLP	19	2.05	4.09	1	0.043	45.94	5.79
% Cov E	20	1.06	2.13	1	0.14	46.77	6.11
% Cov E, SLP	19	2.76	5.53	2	0.063	49.42	5.57
% Cov E, TREAT	20	1.66	3.31	3	0.35	50.56	6.39
SLP, TREAT	19	3.51	7.02	3	0.071	52.62	5.45
% Cov E, SLP, TREAT	19	3.51	7.02	4	0.14	55.13	5.69

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694   [a] –Log likelihood; difference of the log likelihoods of the full and reduced (intercept only) models

695   [b] Likelihood ratio Chi square

696   [c] Degrees of Freedom

697   [d] P value for Likelihood Chi square

698   [e] Akaike Information Criterion corrected for small sample sizes

699   [f] Overdispersion parameter (Pearson Chi square deviance / degrees of freedom of goodness of

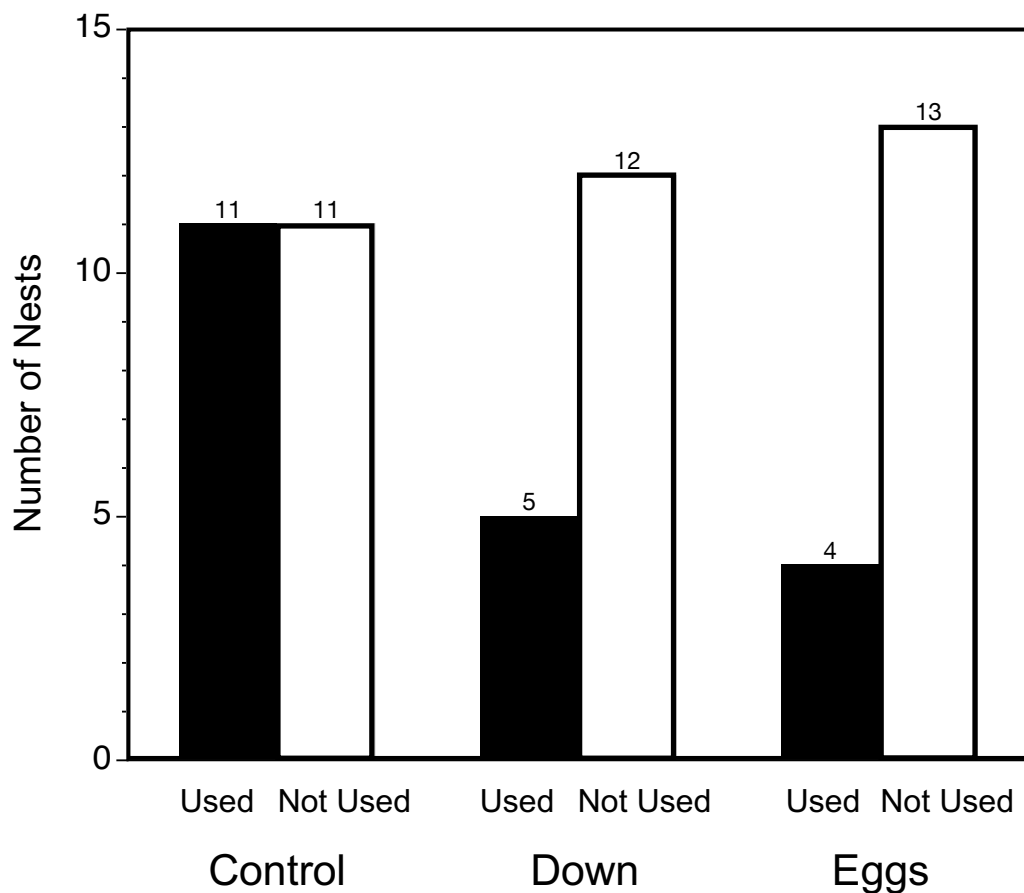700   fit test)

701   [g] Generalized Linear Model, Binomial distribution, Logit link function, corrected for

702   overdispersion

703   [h] Generalized Linear Model, Poisson distribution, Log link function, corrected for overdispersion

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Figures

Fig 1 Use of new nest boxes by wood ducks in California in response to internal visual social cues. New boxes contained down and eggs shells indicating a previously successful hatch (Down), eggs without down indicating current use (Eggs), or shavings indicating no current or previous use (Control). Used boxes are shown by solid black bars, unused boxes are shown by open bars, numbers above provide the number of nests in each category.

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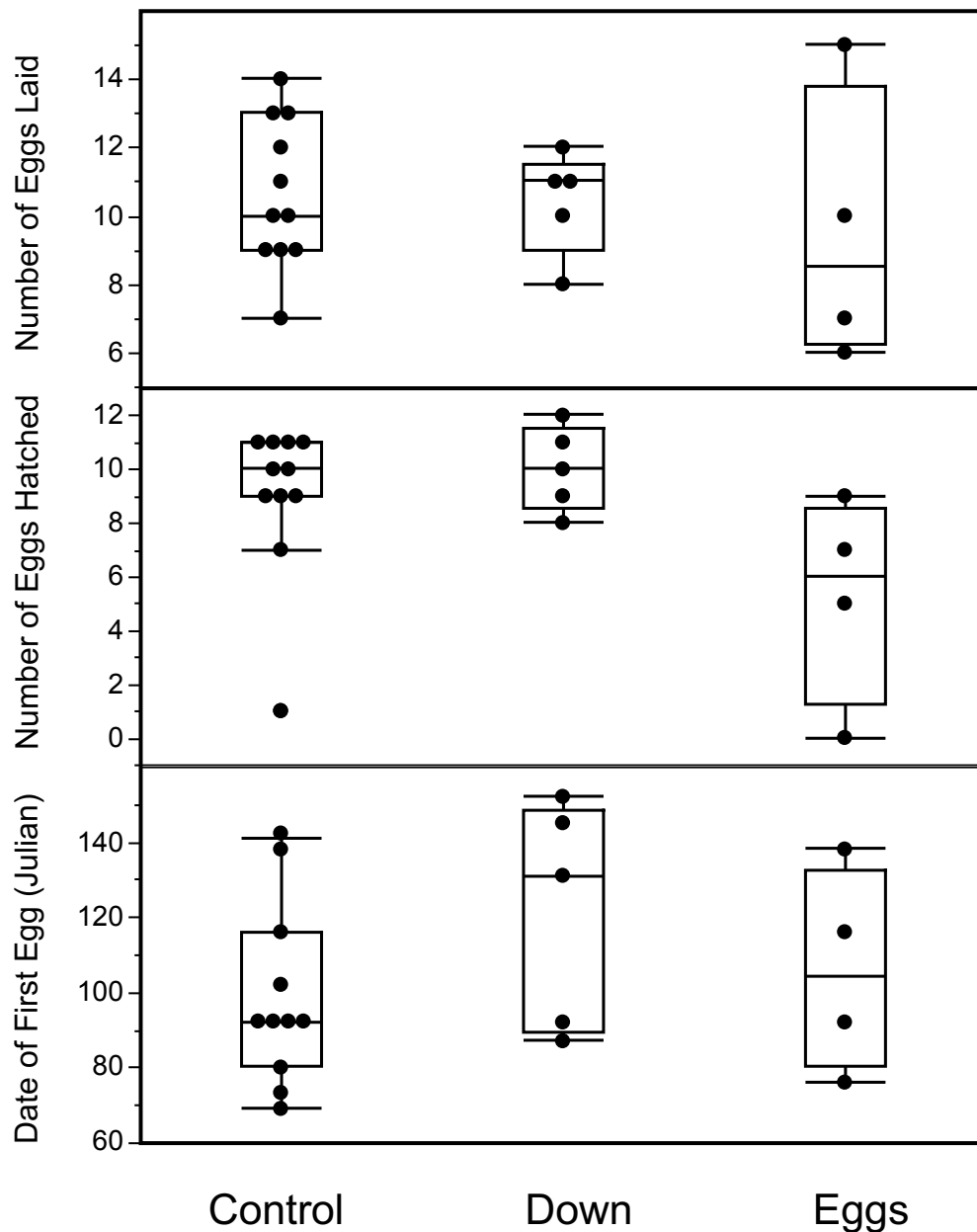
Fig 2 Measures of reproductive success in the three nest box treatment groups

(Control, Down and Eggs). Solid points are values for individual nests with box plots

showing the median, 25th and 75th quantiles (box), and range excluding outliers (vertical

line). Top: Number of eggs laid in each nest, Middle: Number of eggs that hatched in

each nest, and Bottom: Julian date of first egg laid in each nest.

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