Do wood ducks use the quantity of eggs in a nest as a cue to the nest's value?

Nicole S. Odell and John M. Eadie
Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, California 95616, USA

Breeding birds use a variety of cues to choose a nest site. For conspecific brood parasites, the number of eggs in a host nest may be an important indicator of nest stage (laying or incubating) and the resulting prospective value of the nest. In precocial birds, such as wood ducks (*Aix sponsa*), a parasitic female should lay her eggs during the host's laying stage to ensure hatch synchrony with the host. Incubation and hatching success may also be compromised in large clutches. Accordingly, parasitic females should respond to the number of eggs already present in a potential hosts' nest and should preferentially lay eggs in nests with smaller clutches. We conducted a field experiment using simulated nests containing different numbers of "host" eggs to test this hypothesis. When offered a choice of nests containing clutches of 5, 10, 15, or 20 eggs, females were significantly more likely to lay eggs in the 5- and 10-egg treatments, laid more eggs in total in the smaller clutch treatments, and were more likely to incubate the nests in the 5- and 10-egg treatments. These results indicate that wood ducks are responsive to quantitative cues, such as the number of eggs in a nest, although we do not yet know if they are able to do so directly by numerical discrimination (i.e., counting). *Key words: Aix sponsa*, brood parasitism, clutch size, nest site, nest-site cue, wood duck. *[Behav Ecol 21:794–801 (2010)]*

A central assumption in many areas of behavioral ecology is that individuals act as if assessing the profitability of different choices and then use this information to make choices that maximize prospects for success (e.g., mate assessment; Jennions and Petrie 1997 and habitat selection; Jones 2001). In many situations, the differences are qualitative in nature (e.g., brighter, larger, closer). More challenging are cases where the choices differ quantitatively and require some ability to discriminate numerically. Such ability would be valuable when incremental differences in quantity (number) of an item significantly influence the profitability of a choice. The extent to which animals use quantitative cues, possibly involving number sense or counting, has been well studied in the laboratory but has only recently attracted attention in field studies (Shettleworth 2001; Lyon 2003; Emery 2006; Hunt et al. 2008; White et al. 2009).

The phenomenon of avian brood parasitism offers a novel opportunity to examine the extent to which birds may use numerical cues in decision making (Lyon 2003; Low et al. 2009). Brood parasitic species are different from most bird species with parental care because parasites lay their eggs in nests of hosts that already contain eggs. Parasitic individuals are often constrained by the availability of active nests and the limited incubation period of the host; hence, the number of eggs in a nest may provide an important cue on the stage of the nest (laying or incubating) or the host readiness to incubate (Fiorini et al. 2009; Low et al. 2009; White et al. 2009). Furthermore, the prospective value of a nest may vary directly with the number of eggs in a clutch because hatching success is often reduced in large clutch sizes (Bellrose and Holm 1994; Lyon 1998; Soler et al. 1999; Trine 2000). Accordingly,

we might anticipate that parasites would use the number of eggs in a nest to evaluate the potential utility of a particular nest.

Obligate brood parasites rely completely on finding a suitable host nest (because they do not make their own nest) and so may be particularly sensitive to nest cues. For example, brown-headed cowbirds (*Molothrus ater*) examine the host's readiness to incubate by evaluating both the egg-laying rate of the host and the number of host eggs in the nest (Low et al. 2009; White et al. 2009). The state of the nest, such as laying or incubation stage, may also be important for conspecific (nonobligate) brood parasites, particularly so for precocial birds. Evaluating the nest state may allow a female to ensure hatch synchrony with the host (the simultaneous hatching of eggs) that is critical for precocial birds because young that do not hatch with the host eggs will not survive. Nests with small clutch sizes may indicate that a host female has not initiated incubation, and any egg laid in the nest would therefore be synchronized with the host's eggs. Furthermore, the number of eggs in a nest may influence the potential hatching success of the nest, given that large numbers of eggs may inhibit the efficiency of incubation (Semel et al. 1988, 1990; Semel and Sherman 1993, 1995; Bellrose and Holm 1994). Therefore, by laying in a nest with a smaller clutch size, a parasitic female could potentially increase the probability that her egg(s) will hatch.

We explore these ideas here. We examine the extent to which parasitic individuals assess the number of eggs in a nest, and specifically, we predict that parasitic females will prefer nests with smaller clutch sizes due to the higher potential for hatch synchronization and hatch success. We tested this hypothesis using simulated nests containing different clutch sizes. We were also interested in whether females use numerical cues not only to make choices about whether to use a nest but also to modify the number of eggs laid per nest as a function of different clutch sizes. We examined this by evaluating whether females laid different numbers of eggs in a nest-box as a function of the original clutch size and as a function of rate of egg accumulation (how many eggs were laid per day). Because females might also respond to visual cues, such as the visual

Address correspondence to N.S. Odell, Department of Science, Presentation High School, 2281 Plummer Ave, San Jose, CA 95125, USA. E-mail: nicoleodell@att.net.

space the eggs occupy in the nest-box, we also examined whether the number of eggs laid was correlated with the area of the nest-box floor. We predicted that females would lay more eggs in larger boxes assuming that more space was available for eggs, and clutches of equal size would appear smaller in boxes with large floors than boxes with small floors.

Study species

Wood ducks (*Aix sponsa)* are cavity-nesting waterfowl that engage frequently in conspecific brood parasitism. Their natural history has been well documented (Bellrose and Holm 1994; Semel and Sherman 2001), and several studies have investigated qualitative nest-site cues, such as nest-box placement and visibility (Semel et al. 1988; Jansen and Bollinger 1998), and the potential influence of philopatry and kinship (Semel and Sherman 2001; Roy Nielsen et al. 2006). Other qualitative cues, such as nest-site history (Pöysä 2003) and nest-site limitation (Eadie 1991; Pöysä H and Pöysä S 2002), have been well studied in other conspecific brood parasites. As part of a long-term study of this population, we previously explored the effect of nest-site history on nest selection by wood ducks (Roy et al. 2009). We found that females did not select sites based on their own previous success or history at a nest but only on whether a site had been used in the past (Roy et al. 2009). The presence and number of eggs in a nest may provide an important cue on the history and successful use of a site. However, the extent to which wood ducks, or any other conspecific brood parasite, might use quantitative cues such as the number of eggs has largely remained unexplored.

METHODS

Experimental nests

We experimentally manipulated the number of eggs present in a nest-box at the beginning of the breeding season. Our intent was to provide females with a choice of boxes that varied in the number of eggs in the nest. Wooden eggs (Howee's Inc., Joplin, MO), which were similar in size and weight to wood duck eggs, were used to simulate a nest. Wooden eggs were approximately 50.8 mm in length and 34.0 mm in breadth and weighed approximately 40 grams. Wood duck eggs are approximately 50.1 mm in length and 38.2 in breadth and weigh approximately 40.5 g (Kennamer et al. 1997). Wooden eggs were painted beige (KILZ paint, color "Popcorn") to match the most common color of wood duck eggs in our population (Odell NS, personal observation). During 2004, 2 treatments were contrasted; artificial manipulations simulating clutches of small size (5 eggs), and heavily parasitized clutches (20 eggs). Previous studies indicate that a female wood duck typically lays 10–12 eggs in a single clutch (Bellrose and Holm 1994). Nests with 13 eggs or more are considered parasitized (Semel and Sherman 1992).

New nest-boxes (40 boxes, 20 for each condition) were erected to control for previous nest-box history. Each nest-box was built to be the same height from the bottom to the top of the box (37.2 cm) and the same bottom area (547.4 cm^2) of the box to control for spatial cues. Twenty boxes were placed at a site with a high density (38.7 boxes/km) of nest-boxes (Conaway Ranch, Woodland, CA), and 20 boxes were placed at a site with a medium density (18.2 boxes/km) of nest-boxes (Hedgerow Farms, Winters, CA); both sites contained nest-boxes prior to this experiment. Each nest-box was attached to a tree using 2 lag bolts at an approximate height of 1.5 m within sight of water and within 10 m of another nest-box to control for environmental effects on nest-site preferences. The simulated nests contained only shavings and the artificial eggs. The eggs were positioned in the middle of the nest-box on top of the shavings. Nest-site use, the number of eggs, and the nest state (laying or incubating) were recorded weekly. Females were deemed to be incubating when they were on the nest during the day, the eggs were warm, and the eggs were covered in down feathers.

In 2005, 4 treatments were evaluated; (1) clutches of small size (5 eggs, to simulate a situation in which the host is still laying), (2) average (typical) size (10 eggs, simulating a clutch near the completion of egg laying with incubation soon to begin), (3) lightly parasitized nests (15 eggs, in which incubation should have started), and (4) heavily parasitized (20 eggs, in which incubation should have started or the nest is abandoned). A heavily parasitized nest would represent a nest where either several parasitic females had laid eggs or 1 parasitic female laid her whole clutch in the box.

Nest-boxes from 2004 ($n = 40$) were reused for the experiment in 2005, and 20 new boxes were erected at Conaway Ranch to increase sample size (total nest-boxes = 60). New nest-boxes were similar but larger than the previously erected boxes (bottom of box area was 726.3 cm^2). Treatments were randomly assigned among boxes to control for previous nest-box history, nest-box size, and philopatry.

Female wood ducks cover their eggs during absences from the nest, both before and during incubation (Bellrose and Holm 1994). As artificial eggs were placed uncovered in nest-boxes, changes in egg position in the nest indicated that a female had investigated the nest. During each nest-box visit, we recorded any visual changes in egg position, such as whether eggs were buried in shavings or uncovered. This provided an additional means by which to assess whether females visited and assessed experimental treatments, even when egg laying did not occur. We caution that we cannot determine with absolute certainty that all movements of eggs were by wood duck females. Predators or other bird species may have inspected the boxes. However, predation on nests is uncommon in this population (Roy et al. 2009), and predation attempts were typically indicated by egg loss, destruction, or marks (e.g., tooth or bill marks) on eggs. Extended observational watches at nest-boxes indicated that only wood ducks entered nest-boxes during this period of the year. Accordingly, changes in egg position could not be readily attributed to other species.

Non–experimental nests

We also followed a large number of non–experimental nests. These were nests where birds selected a nest-box under natural conditions (no manipulation or other interference). We collected data on these nests during 7 field seasons (2000–2006) to compare the behavior of birds in our clutch size experiment with natural patterns of egg laying.

Nest checks were performed at least biweekly throughout the nesting season (February–August) at 4 field sites: (1) Conaway Ranch (lat 38°386N, long 123°420W, USA), (2) Putah Creek (lat 38°310N, long 121°465W, USA), (3) Hedgerow Farms (lat 38°360N, long 121°590W, USA), and (4) Russell Ranch (lat 38°323N, long 121°525W, USA). Each site encompassed 2–5 km of riparian habitat along a stream (Putah Creek, Russell Ranch) or slough (Conaway ranch, Hedgerow farms). During nest checks, females were identified via United States Geological Services' metal leg bands, and eggs were counted, numbered, weighed, and measured. Hatching success (number of ducklings hatched) was determined by subtracting the number of ducklings hatched from the final clutch size.

As the nest-boxes of the natural nests were not uniform, we examined the potential relationship of nest-box size and clutch sizes. The bottoms of nest-boxes were measured for width and

length (cm). Area was estimated by multiplying width by length.

Statistical analysis

We first used contingency tests (log likelihood chi square) to test for differences among study sites (Conaway Ranch, Hedgerow Farms) and years (2004 and 2005) in the response of wood ducks to the experimental treatments. Our response variable in each test was type of nest use (incubated, egg laid but not incubated, and not used). As there were no differences among sites (likelihood ratio $\chi^2 = 4.88$, degrees of freedom [df] $= 2$, $P = 0.09$) or years (likelihood ratio $\chi^2 = 2.50$, df $= 2$, $P = 0.29$) in the type of use of boxes with experimental treatments, we pooled data for all study sites and years.

We also used contingency tests (log likelihood chi square) to evaluate female use of boxes with different treatments (again indicated by type of use—incubated, egg laid but not incubated, and not used). We further compared the types of use (laid in only versus incubated) using contingency tests. Differences in the number of eggs laid per treatment were examined using one-way analysis of variance (ANOVA). We refer to 2 measures of clutch size: (1) only the eggs laid by females (hereafter "added" eggs) and (2) total clutch size, which includes both the added eggs and the original experimental artificial eggs (this would reflect the total number of eggs in the nest visible to a visiting female).

For all boxes that were used, we plotted the laying behavior of females in each box. We calculated the total clutch size of each nest, the number of eggs laid per box, the length of time the box was being used (egg-laying activity), and the rate of egg laying. We used one-way ANOVA to compare each response variable among treatments. Egg deposition rates were calculated by dividing the number of eggs laid in a box by the number of days the nest was active. Lag times were calculated as the number of weeks between the start of the experiment and the week the first egg was laid; differences in lag times between treatments were compared using ANOVA.

As a second method to evaluate whether females differed in their response to the experimental treatments, we used contingency analysis to compare the number of nest-boxes with eggs covered with shavings (indicating a female visit to the box) with the number of nest-boxes where the eggs remained uncovered.

We examined the relationship between clutch sizes and nest-box area using simple linear regression, and we contrasted the clutch sizes of experimental to non–experimental nests using t-tests. We examined the relationship between clutch sizes and hatching success (proportion of eggs hatching) using second order polynomial regression. In all cases where we used parametric statistics (ANOVA or t-tests), we first tested for departures from normalcy using the Shapiro–Wilk test and unequal variances using the Levene test, respectively; our data were robust to these assumptions. Analyses using nonparametric tests provided the same conclusions. Analyses were conducted using JMP, Version 7. SAS Institute Inc., Cary, NC, 1989–2007.

RESULTS

Do wood ducks respond to the number of eggs in a nest?

In experimental boxes, females were more likely to lay eggs in nests with smaller clutches (likelihood ratio $\chi^2 = 19.75$, df $= 3$, $P < 0.001$), with use ranging from 60% of 5-egg treatments to 10% of 20-egg treatments (Figure 1). The degree of use declined in direct relation to the number of experimental eggs present in the box (Spearman rank correlation of proportion of nests used vs. number of experimental eggs: $r_s = -0.83$, $P <$
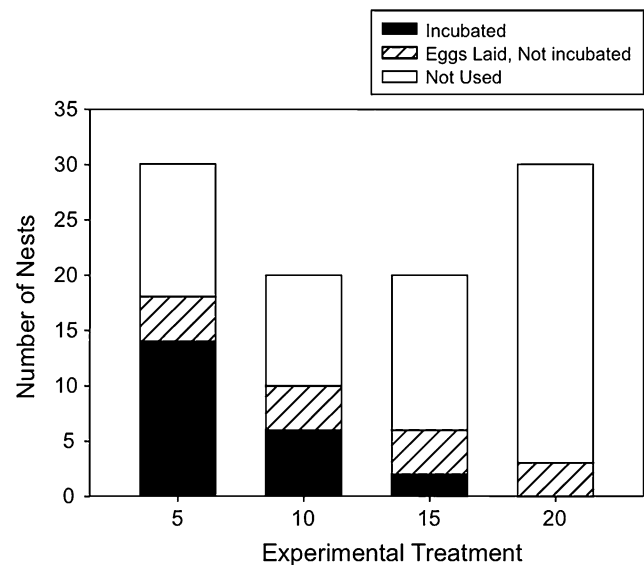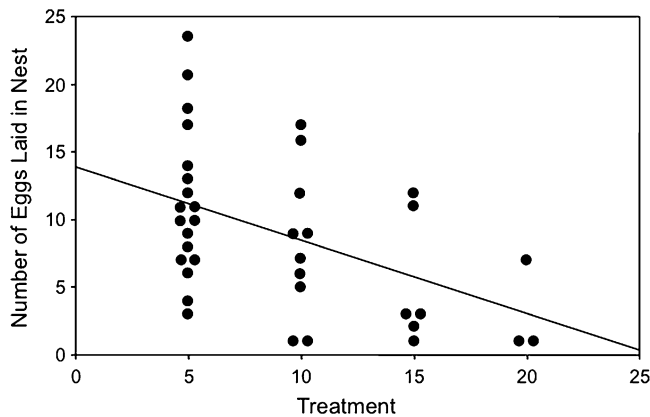

Figure 1
Types of use by experimental treatment. This figure shows the number of boxes that were not used (no eggs were laid), the number of boxes where an egg was laid, and the number of boxes where female(s) laid an egg in the box and incubated the nest.

0.003; Figure 1). The type of response (not used, eggs laid but not incubated, eggs laid, and incubated) also differed significantly among the 4 treatments (likelihood ratio $\chi^2 = 29.54$, df $= 3$, $P < 0.0001$; Figure 1). Small experimental clutches were more likely to be used and incubated, whereas large experimental clutches were less likely to be used or incubated (Figure 1). Considering only the subset of boxes that were used (i.e., at least 1 egg laid), the degree to which females incubated nests varied among the 4 treatments (likelihood ratio $\chi^2 = 9.79$, df $= 3$, $P < 0.02$; Figure 1). Females incubated nests in the smaller experimental clutches significantly more often than larger clutches (Spearman rank correlation of proportion of nest incubated (of those used) versus number of experimental eggs: $r_s = -0.90$, $P < 0.001$). Females did not incubate any of the nests in the 20-egg treatment.

As a second assessment of the response to the clutch size treatments, we compared visual changes in the arrangement of eggs in the box (covered in shavings or uncovered). All treatments exhibited evidence of having being explored by females; over half of all nests (53 of 100) had eggs covered in shavings at some point. However, we found significant differences among treatments in the degree to which females covered eggs (likelihood ratio $\chi^2 = 24.65$, df $= 3$, $P < 0.001$). A majority of the 5-egg nests (67%, 20 of 30), 10-egg nests (75%, 15 of 20), and 15-egg nests (65%, 13 of 20) exhibited evidence of covering, but only 17% (5 of 30) of the 20-egg nests showed evidence of egg covering. Post hoc tests revealed that the difference among the 5-, 10-, and 15-egg treatment was not significant when the 20-egg nests were excluded (likelihood ratio $\chi^2 = 0.57$, df $= 2$, $P > 0.75$).

Do females modify the number of eggs they lay as a function of the number of eggs in a nest?

The average number of eggs laid in experimental boxes differed significantly among treatments ($F = 3.37$, df $= 3, 33$, $P = 0.03$). More eggs were laid in the smaller clutch treatments (Figure 2) as the number of eggs per treatment declined in direct relation to the number of experimental
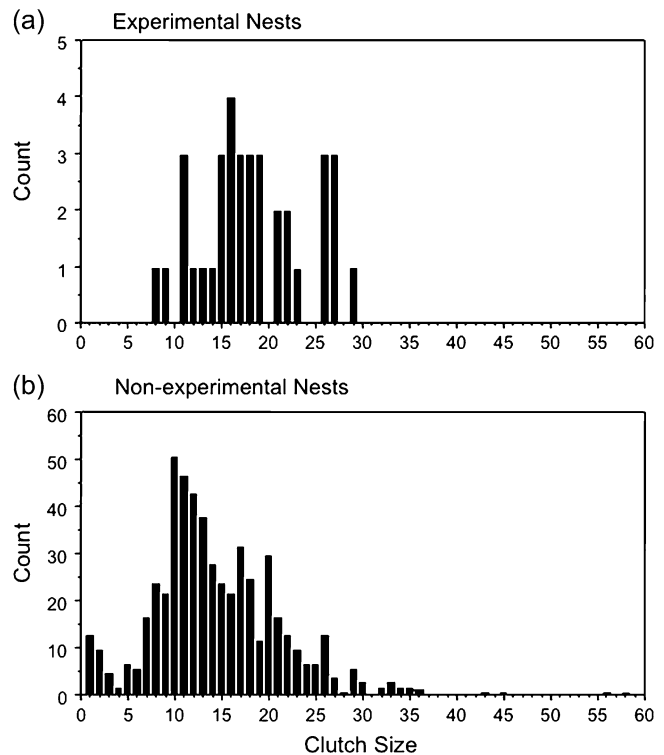
Figure 2
Total clutch sizes by experimental treatment. The *x* axis shows the experimental treatments. The *y* axis shows the total number of eggs laid by females in each box. The regression line illustrates the decline in the number of eggs laid by females in each successive experimental treatment.

Figure 3
Frequency distribution of clutch sizes. (A) Clutch sizes in experimental nests (artificial eggs plus "added" eggs) and (B) clutch sizes of non–experimental nests in our populations.

eggs in each treatment (mean ± standard error [SE]: 5-egg treatment: 11.4 ± 1.3, $n = 18$; 10-egg treatment: 8.3 ± 1.7, $n = 10$; 15-egg treatment: 5.3 ± 2.2, $n = 6$; and 20-egg treatment: 3.0 ± 3.1, $n = 3$). Linear regression of the number of eggs laid against the number of experimental eggs in each treatment suggests that for each incremental experimental egg, approximately 0.58 fewer eggs were laid by wood duck females (regression equation: $14.23 - 0.58 \times$ No. Eggs in Treatment; $F = 10.68$, df = 1, 35, $P < 0.003$). In contrast, the total number of eggs (i.e., "added" by females plus experimental) did not differ significantly among treatments ($F = 1.80$, df = 3, 33, $P > 0.15$), suggesting that there may be an upper limit to the number of eggs that females will lay in a nest site.

Although females clearly differed in the number of eggs added to each treatment, the rate at which they did so did not differ among treatments. Egg addition rates (the number of eggs added per day) of the manipulated treatments did not differ significantly ($F = 0.80$, df = 3, 29, $P > 0.50$; mean eggs/day ± SE: 5-egg treatment: 0.39 ± 0.08, 10-egg treatment: 0.48 ± 0.10, 15-egg treatment: 0.29 ± 0.12, and 20-egg treatment: 0.20 ± 0.18). Likewise, the lag time (number of weeks between the start of the experiment and the week the first egg was laid) did not differ significantly among treatments ($F = 0.80$, df = 3, 33, $P > 0.50$; mean lag ± SE: 5-egg treatment: 5.3 weeks ± 1.8, 10-egg treatment: 9.3 ± 2.6, 15-egg treatment: 8.7 ± 2.9, and 20-egg treatment: 4.0 ± 4.5).

Are experimental nests similar to non–experimental nests?

Unmanipulated clutch sizes of wood ducks in our population varied considerably from 1 to 58 eggs but most nests ranged from 6 to 27 eggs (Figure 3). Experimental nests contained total clutch sizes between 8 and 29 eggs when artificial eggs were included (Figure 3). Considering only eggs added to nests (excluding experimental eggs), the average number of eggs in experimental nests was significantly less than that in non–experimental nests ($t = 2.82$, df = 151, $P < 0.01$; mean ± SE experimental nests: 8.9 ± 1.1, $n = 37$; and non–experimental nests: 12.3 ± 0.6, $n = 116$). However, when we included the experimental eggs, the total clutch size in experimental nests (18.0 ± 1.0) was significantly greater than that in unmanipulated nests ($t = 4.73$, df = 151, $P < 0.001$). Hence, females laid fewer eggs in total in experimental nests relative to non–experimental nests, but the total "apparent"

clutch size was larger. It is noteworthy that even in the experimental nests, total clutch sizes rarely exceed 25 eggs, despite the finding that several of these nests started with 15–20 experimental eggs at the outset (Figure 3).

Hatching success of eggs varied significantly with clutch size in non–experimental nests (polynomial regression, $r^2 = 0.073$, $F = 21.67$, df = 552, $P < 0.001$; regression equation: Hatching Success = $0.2722 + 0.369 \times$ Clutch Size $- 0.0009 \times$ Clutch Size^2, first and second order terms significant; $P < 0.001$). Hatching success was lowest in both very small clutches, due to high rates of nest abandonment by female, and in very large clutches due largely to reduced hatching success of some eggs in the clutch, although some very large clutches (>40 eggs) were never incubated (Figure 4).

Are females responding to a spatial or a visual cue?

Females did not appear to respond to the overall size of the box or the degree to which eggs might be visually "concentrated" in smaller boxes. There was no relationship between the number of eggs laid in a nest site and the floor area of the nest-box ($r^2 = 0.002$, $F = 0.66$, df = 439, $P > 0.40$; Figure 5).

DISCUSSION

Assessment of clutch size

Female wood ducks appear to be capable of assessing relative quantities, such as the number of eggs in a nest, to distinguish among nest sites. Females were more likely to lay eggs in nests with smaller clutches and laid more eggs in these nests than in those containing larger clutches. Although females explored all treatments as suggested by the signs of females burying eggs in shavings, females chose to parasitize and incubate smaller
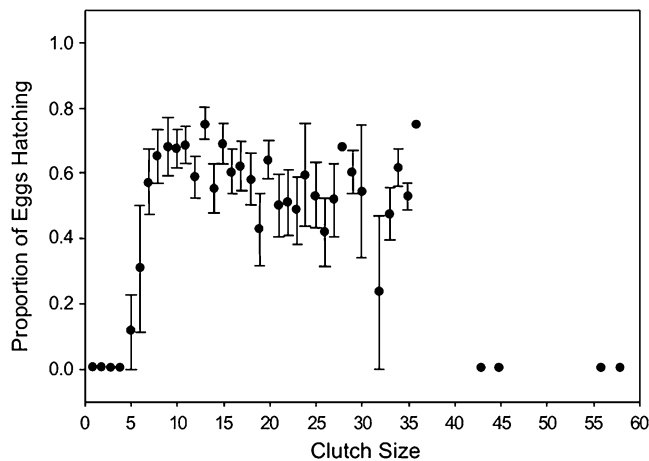
Figure 4
Hatching success (proportion of eggs that hatch) as a function of clutch sizes in non–experimental nests.

nests. This suggests that females may have actively compared the content of nests and retained that information for use in laying decisions. Retaining quantitative information is not uncommon in birds, particularly in food-hoarding species (Hunt et al. 2008). Wood ducks also have the potential for retaining and comparing information, as seen by our previous study of nest-site histories and public information (Roy et al. 2009).

Female wood ducks may have the ability to not only discern large differences in magnitude as suggested by the nest choice preferences in our experiment but also may have a more refined ability to alter their individual egg-laying and reproductive behavior—females allocated their eggs differentially depending on the current clutch size of the nest. Although laying rates were not significantly different across treatments, females laid more eggs in total in nests with the smaller clutch sizes. Furthermore, the number of eggs in the nest not only affected how many eggs females laid but also whether females committed to incubating the nest. Some females, despite the fact that other eggs were already present, incubated nests with

a small number of eggs. These results suggest that the clutch size is informative not only for parasitic females but also for females searching for their own nest site (Shaw and Hauber 2009).

Females were clearly responsive to an upper limit of eggs in a nest-box. If females were simply laying eggs in a site without regard to the number of eggs already in the nest, we would expect nests to simply accumulate eggs until the end of the reproductive season, resulting in very large clutch sizes. However, all 4 treatments had similar total clutch sizes (artificial eggs plus added eggs) and ceased accumulating eggs after reaching 27 eggs, suggesting an upper threshold beyond which females are unwilling (or less willing) to surpass. If individuals did not evaluate, in some way, the number of eggs in a nest, we would not expect to reach such a threshold. Furthermore, experimental nests and non–experimental nests had similar total clutch sizes even though the nests were available for different amounts of time. Most non–experimental clutches were available only for a limited number of days before the nest owner began incubation, limiting the number of eggs that could be added by other females. In contrast, most experimental nests were available for use throughout the nesting season (excluding those where a female incubated the clutch). Despite these differences, experimental and non–experimental nests reached similar thresholds and exhibited similar clutch size distributions. Finally, we found little evidence of difference in egg-covering behavior (an indication that females actively explored nest sites and potentially were preparing to lay eggs) in the 5-, 10-, and 15-egg treatments, yet egg covering was markedly reduced in the 20-egg treatments, suggesting that females actively discriminated against boxes containing large clutches.

Our study is potentially complicated by the laying and behavioral "decisions" of multiple females—some females may have laid eggs in more than 1 box, whereas conversely, several different females may have laid eggs in the same box. The statistical implications of the former are that each site may not be fully independent, and we would have overestimated the sample size of independent responses. On the other hand, the response observed at any single site would effectively be a "pooled" response (of several females), and we would have underestimated the independent choices of individual females. These effects (one potentially inflating sample size
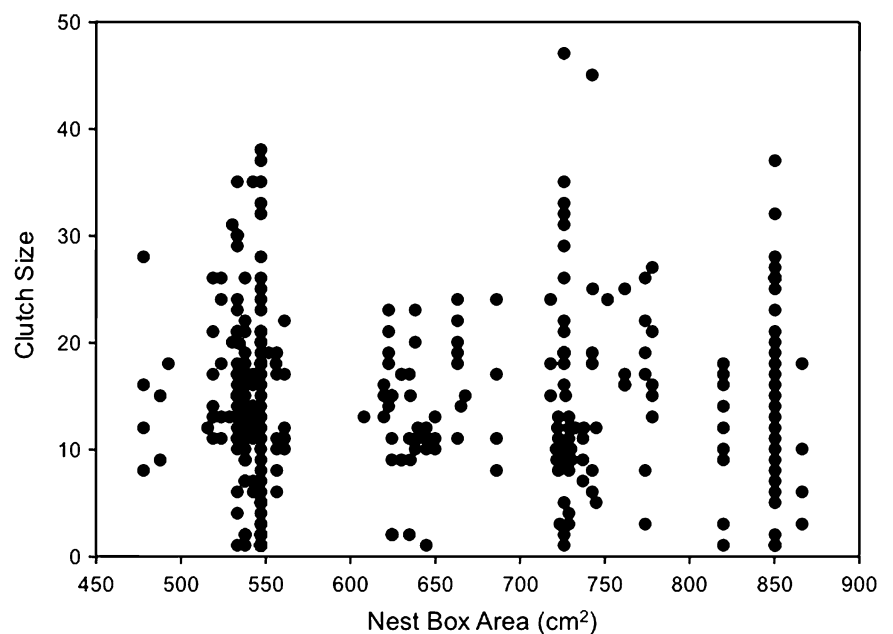
Figure 5
The relationship of clutch size to area of the nest-box in un-manipulated nests. Nest-box area was calculated by multiplying the box width by the box length—the area that would be available for a single layer of eggs in the box.

and the other reducing sample size by pooling) would tend act in opposite directions with respect to statistical power and may cancel. In any case, without a detailed genetic analysis of the maternity of each egg (beyond the scope of the current study), we could not identify eggs of individual females. A conservative approach in the absence of such information was to treat each box as the independent unit of study (and indeed, this was how we designed the experiment). The patterns we observed were highly significant, suggesting that our results are robust even with a more conservative approach. A further complication is that, if multiple females lay in the same experimental nest, the eggs laid by the other females then become part of the current clutch size to which a new female might respond. This would likely act to obscure the differences among our original clutch size treatments and so again our results are conservative. Despite this, clear patterns persisted even in the face of such possible "blending" effects among treatments.

Possible mechanisms for assessment

The means by which females are able to assess the number of eggs in a nest remains unclear, although we envision at least 3 potential mechanisms: numerical discrimination, tactile stimulation, and visual cues. Numerical discrimination has been shown to play a potential role in a variety of choices that affect an individual's success, such as assessing foraging options and selection of food patches (Uller et al. 2003; Farnsworth and Smolinski 2006; Stevens et al. 2007; Hunt et al. 2008), evaluating the group size of conspecifics to reduce individual predation risk (Agrillo et al. 2008) and selecting prey by their numerical abundance (Krause and Godin 1995). Historically, most research on numerical discrimination has been completed in the laboratory (Boysen and Hallberg 2000; Hauser et al. 2000; West and Young 2002; Cooper et al. 2003), although more recent studies have started to explore the importance of cognitive ability in the wild (Shettleworth 2001; Lyon 2003; Emery 2006; Hunt et al. 2008). Evidence from other egg-laying species (Armstrong and Robertson 1988; Beukeboom et al. 1988; Bauchau and Seinen 1997; Lyon 2003; White et al. 2009) suggests that female birds may use clutch size in a variety of reproductive decisions and may, in fact, be able to count. Common goldeneye ducks (*Bucephala clangula*) and common eiders (*Somateria mollisima*) reduce their own clutch size in response to parasitic eggs being laid in their nest (Andersson and Eriksson 1982; Erikstad and Bustnes 1994; Hauber 2003). Crèching behavior and brood abandonment in Barrow's goldeneye (*B. islandica*) and common goldeneye are dependent on the number of offspring in a brood, suggesting that females can assess and evaluate the value of a particular brood size (Eadie and Lyon 1998; Pöysä H and Pöysä S 2002; Pöysä 2003).

Although evidence for true counting in birds is limited, a recent study by White et al. (2009) (and see Low et al. 2009) demonstrates a refined ability of brown-headed cowbirds to assess both the quantity of eggs in a nest and the egg-laying rate of the host species. Cowbirds were able to discern differences between small clutch sizes of eggs. More remarkably, cowbirds also appeared to be able to detect changes in the number of eggs in a nest between visits and spent more time inspecting nests when the accumulated number of eggs matched that expected by the number of days elapsed between visits; in other words, they appeared to be sensitive to violations of rules of addition (i.e., 1 egg + 1 egg = 1 egg; see review in Low et al. 2009). Another species, the New Zealand robin (*Petroica australis*), also appeared to be sensitive to violations of rules of addition (Hunt et al. 2008), suggesting the ability to detect small differences in quantity. Other species, including mosquitofish (*Gambusia affinis*) (Agrillo et al. 2006),

dogs (*Canis familiaris*) (Sulkowski and Hauser 2001; Cooper et al. 2003), parrots (*Psittacus erithacus*) (Pepperberg 2006), pigeons (*Columba livia*) (Roberts et al. 2002), honeybees (*Apis mellifera*) (Dacke and Srinivasan 2008), macaques (*Macaca mulatta*) (Washburn and Rumbaugh 1991; West and Young 2002), and human infants (*Homo sapien*) (Wynn 1992), have also been shown to have some degree of numerical discrimination or counting. The fact that female wood ducks appeared to adjust not only their use of nest sites but also the number of eggs they lay in those sites as a function of the number of eggs already present suggests that some means of numerical discrimination may be used to assess clutch size.

An alternative hypothesis to explain the differences in egg laying and nest use of our manipulated treatments is that, rather than using numerical cues, females simply assess the area occupied by eggs in the nest-box. If so, then we would expect to find that fewer eggs would be laid in smaller nest-boxes with less area available. Large boxes with the same number of eggs would appear to have more space available for additional eggs, or the clutch may appear smaller. Yet, despite the large range in the size of our nest-boxes, the number of eggs laid by females did not correlate with box size. In contrast to our study, Stephens et al. (1998) found that larger wood duck boxes contained more eggs than smaller boxes. However, their study involved a newly established population with birds selecting nest sites for the first time. The higher number of eggs in the large boxes may simply reflect a preference by females for nesting in large boxes. Nonetheless, the contrasting patterns found in our studies suggest that the "apparent size" of the clutch may yet play a role in nest-site selection behavior.

A final possibility is that females respond simply to the tactile stimulation of the brood patch provided by the number of eggs in the nest (Haywood 1993). Tactile stimulation has been shown to impact the onset of incubation and clutch termination in some birds and also in some hosts of brood parasites (Rothstein 1986; Book et al. 1991; Haywood 1993). Although this remains a possibility for wood ducks, we note that it would nonetheless require a fairly refined ability of females to adjust egg-laying behavior rapidly and on a site-specific basis. Parasitic females often visit several different nests in a single morning (Odell NS, personal observation) and so would potentially receive conflicting tactile cues during a relatively short time. Possibly, females are able to detect the number of eggs in a nest simply by sitting on the eggs and quickly sensing how much of their body is in contact with eggs. As such, we cannot currently determine the role tactile stimulation may play in assessing clutch size. Furthermore, tactile and visual stimulation may not be mutually exclusive. For example, one can count jelly beans in a dish visually as well as by closing one's eyes and feeling with one's fingers (we thank an anonymous reviewer for suggesting this analogy). Therefore, even if wood ducks are not able to visually discern the number of eggs in a dark nest cavity or nest-box, females could nonetheless count or assess the number of eggs using tactile stimulation.

Why might the number of eggs be a valuable cue?

Parasitic individuals could benefit substantially if they were able to assess the number of eggs in a potential host nest. By doing so, a brood parasite may be able to better evaluate the laying stage and/or prospective value of a nest. The value of a nest may be impacted by hatch synchrony with the host's eggs, which is critical for precocial birds, as young leave the nest almost immediately after hatching. Parasitic females should deposit parasitic eggs prior to the start of incubation by the host to eliminate asynchronous hatching (Semel et al. 1988, 1990; Semel and Sherman 1993, 1995; Bellrose and Holm 1994).

Larger clutch sizes may also indicate that a nest has been abandoned, is closer to incubation, is already being incubated, or may be incubated less efficiently. The number of eggs in a nest can also impact hatch success, presumably by reducing the incubation efficiency of large clutches (Semel et al. 1988, 1990; Semel and Sherman 1993, 1995; Bellrose and Holm 1994). Choosing a host nests with a smaller clutch could benefit a parasite if hatch success is higher and results in an increased probability of the parasitic egg(s) hatching. Although we did not manipulate nests to have less than 5 eggs, very small nests (5 or less) may be drop nests, which are characterized by 1–6 eggs that are not incubated and are abandoned (Morse and Wright 1969). The hatch success of non–experimental nests in our populations is low at these clutch sizes, typically (0% to 10%), suggesting that very small clutch sizes are not desirable either.

The ability to assess clutch size might also be valuable to females seeking a nest of their own to eventually incubate (rather than parasitize). Females apparently are willing to use or "take over" nests that have already been used by other females (i.e., contain eggs). In this case, females might assess clutch size to evaluate the costs of taking over, with larger clutches being more costly due to lower hatch success (Bellrose and Holm 1994). Semel and Sherman (2001) reviewed several hypotheses on why brood parasitism occurs, including the hypothesis that females are not intentionally parasitic but instead are simply competing for a valuable nest site. Nests with a small number of eggs may be sufficiently valuable that females incubate the nest, despite the fact that other eggs are already present (Thomson et al. 1998). Perhaps, smaller clutches indicate that a putative host female is less established, and the prospects of winning the nest are greater than if the clutch size was large. Clutch size may therefore serve as a cue on the probability of a successful nest takeover attempt.

Lyon (2003) provided evidence that American coots (*Fulica americana*) count eggs. Coots apparently manipulate clutch sizes by rejecting parasitic eggs or exiling the parasitic eggs to the perimeter of the nest and thereby reduce the fitness costs of brood parasitism. Female wood ducks may not be able to reject parasitic eggs easily due to the constraints of being in a cavity nest—eggs may be more difficult to differentiate in the dark interior, and any egg removal must occur by being carried out of the nest rather than being rolled out. Assessing clutch size, either by counting or another mechanism, would provide a means by which host females could decide when to continue to invest in a nest and when to abandon. Therefore, whether as hosts or parasites, female wood ducks could benefit considerably from the ability to assess clutch size when making decisions that may greatly impact their reproductive success.

Although we cannot yet determine the mechanism by which female wood ducks are able to assess the number of eggs in a nest, it is clear that they are able to do so. If wood ducks are capable of numerical discrimination, it would be of interest to understand further the rules by which they might do so. Cognitive psychologists have identified 2 core systems of numbers that appear to function in humans and possibly other animals: one system functions to recognize large approximate numerical magnitudes, whereas a second system appears to enable more precise representation of small numbers of individual objects (Feigenson et al. 2004). Both systems have been detected in other species, although much of this work has focused on primates and rats in the laboratory. To achieve the level of discrimination suggested by our study, wood ducks might only need to be able to determine numerical differences of relatively large magnitude (e.g., differences in clutch size of 5 eggs). The functional value of a more refined counting skill may be limited given that only small changes in reproductive success (hatching success) occur with small increments in total clutch size (Figure 4). Indeed, a large number system sensitive to ratio (10 vs. 5 eggs = 1.2 and 15 vs. 5 eggs = 1.3) could adequately explain the results we observed, without invoking a more precise number sense. As White et al. (2009) and Low et al. (2009) have recognized, avian brood parasites may prove to be model systems to investigate avian cognition in the wild, given the need to time laying appropriately to the host and the potential utility of choosing host nests with smaller number of eggs. Future studies to explore the apparent numerical abilities of these species may add to the growing list of animals that have been shown to exhibit a number sense in the wild.

REFERENCES

Agrillo C, Dadda M, Bisazza A. 2006. Quantity discrimination in female mosquitofish. Anim Cogn. 10:63–70.

Agrillo C, Dadda M, Serena G, Bisazza A. 2008. Do fish count? Spontaneous discrimination of quantity in female mosquitofish. Anim Cogn. 11:495–503.

Andersson M, Eriksson MOG. 1982. Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. Am Nat. 120:1–16.

Armstrong T, Robertson RJ. 1988. Parental investment based on clutch value: nest desertion in response to partial clutch loss in dabbling ducks. Anim Behav. 36:941–943.

Bauchau V, Seinen I. 1997. Clutch desertion and re-nesting in pied flycatchers: an experiment with progressive clutch removal. Anim Behav. 54:153–161.

Bellrose FC, Holm DJ. 1994. Ecology and management of the wood duck. Mechanicsburg (PA): Stackpole Books.

Beukeboom L, Dijkstra C, Daan S, Meijer T. 1988. Seasonality of clutch size determination in the kestrel Falco tinnunculus: an experimental approach. Ornis Scand. 19:41–48.

Book CM, Millam JR, Guinan MJ, Kitchell RL. 1991. Brood patch innervation and its role in the onset of incubation in the turkey hen. Physiol Behav. 50:281–285.

Boysen ST, Hallberg KI. 2000. Primate numerical competence: contributions toward understanding nonhuman cognition. Cogn Sci. 24:423–443.

Cooper JJ, Ashton C, Bishop S, West R, Mills DS, Young RJ. 2003. Clever hounds: social cognition in the domestic dog (*Canis familiaris*). Appl Anim Behav Sci. 81:229–244.

Dacke M, Srinivasan MV. 2008. Evidence for counting in insects. Anim Cogn. 11:683–689.

Eadie JM. 1991. Constraint and opportunity in the evolution of brood parasitism in waterfowl. Acta Congr Int Ornithol. 20:1031–1040.

Eadie JM, Lyon BE. 1998. Cooperation, conflict, and creching behavior in goldeneye ducks. Am Nat. 151:397–408.

Emery NJ. 2006. Cognitive ornithology: the evolution of avian intelligence. Philos Trans R Soc Biol Sci. 361:23–43.

Erikstad KE, Bustnes JO. 1994. Clutch size determination in common eiders: an egg removal and egg addition experiment. J Avian Biol. 25:215–218.

Farnsworth GL, Smolinski JL. 2006. Numerical discrimination by wild northern mockingbirds. Condor. 108:953–957.

Feigenson L, Dehaene S, Spelke E. 2004. Core systems of numbers. Trends Cogn Sci. 8:307–314.

Fiorini VD, Tuero DT, Reboreda JC. 2009. Shiny cowbirds synchronize parasitism with host laying and puncture eggs according to host characteristics. Anim Behav. 77:561–568.

Hauber ME. 2003. Interspecific brood parasitism and the evolution of host clutch sizes. Evol Ecol Res. 5:559–570.

Hauser MD, Carey S, Hauser LB. 2000. Spontaneous number representation in semi-free-ranging rhesus monkeys. Proc R Soc Lond B Biol Sci. 267:829–833.

Haywood S. 1993. Sensory and hormonal control of clutch size in birds. Q Rev Biol. 68:33–60.

Hunt S, Low J, Burns KC. 2008. Adaptive numerical competency in a food-hoarding songbird. Proc R Soc Lond B Biol Sci. 275: 2373–2379.

Jansen RW, Bollinger EK. 1998. Effects of nest-box visibility and clustering on wood duck brood parasitism in Illinois. Trans Ill State Acad Sci. 91:161–166.

Jennions MD, Petrie M. 1997. Variation in mate choice and mating preferences: a review of causes and consequences. Biol Rev. 72: 283–327.

Jones J. 2001. Habitat selection studies in avian ecology: a critical review. Auk. 118:557–562.

Kennamer RA, Alsum SK, Colwell SV. 1997. Composition of wood duck eggs in relation to egg size, laying sequence, and skipped days of laying. Auk. 114:479–487.

Krause J, Godin J-GJ. 1995. Predator preferences for attacking particular group sizes: consequences for predator hunting success and prey predation risk. Anim Behav. 50:465–473.

Low J, Burns KC, Hauber ME. 2009. Wild number sense in brood parasitic brown-headed cowbirds. Ibis. 13. 775–777.

Lyon BE. 1998. Optimal clutch size and conspecific brood parasitism. Nature. 392:380–383.

Lyon BE. 2003. Egg recognition and counting reduce costs of avian conspecifics brood parasitism. Nature. 422:495–499.

Morse TE, Wright HM. 1969. Dump nesting and its effect on production in wood ducks. J Wildl Manage. 33:284–293.

Pepperberg IM. 2006. Cognitive and communicative abilities of grey parrots. Appl Anim Behav Sci. 100:77–86.

Pöysä H. 2003. Parasitic common goldeneye (*Bucephala clangula*) females lay preferentially in safe neighborhoods. Behav Ecol Sociobiol. 54:30–35.

Pöysä H, Pöysä S. 2002. Nest-site limitation and density dependence of reproductive output in the common goldeneye *Bucephala clangula*: implications for the management of cavity-nesting birds. J Appl Ecol. 39:502–510.

Roberts WA, Roberts S, Kit KA. 2002. Pigeons presented with sequences of light flashes use behavior to count but not to time. J Exp Psychol Anim Behav Process. 28:137–150.

Rothstein SI. 1986. A test of optimality: egg recognition in the eastern phoebe. Anim Behav. 34:1109–1119.

Roy C, Eadie JM, Schauber EM, Odell NS, Berg EC, Moore T. 2009. Public information and conspecific nest parasitism in wood ducks: does nest density influence quality of information? Anim Behav. 77:1367–1373.

Roy Nielsen C, Semel B, Sherman PW, Westneat DF, Parker PG. 2006. Host-parasite relatedness in wood ducks: patterns of kinship and parasite success. Behav Ecol. 17:491–496.

Semel B, Sherman PW. 1992. The use of clutch size to infer brood parasitism in wood ducks. J Wildl Manage. 56:495–499.

Semel B, Sherman PW. 1993. Answering basic questions to address management needs: case studies of wood duck nest box programs. Transactions of the North American Wildlife and Natural Resources Conference; 1993 Mar 19–24; Washington (DC). Wildlife Management Institute. 58:537–550.

Semel B, Sherman PW. 1995. Alternative placement strategies for wood duck nest boxes. Wildl Soc Bull. 23:463–471.

Semel B, Sherman PW. 2001. Intraspecific parasitism and nest-site competition in wood ducks. Anim Behav. 61:787–803.

Semel B, Sherman PW, Byers SM. 1988. Effects of brood parasitism and nest-box placement on wood duck breeding ecology. Condor. 90:920–930.

Semel B, Sherman PW, Byers SM. 1990. Nest boxes and brood parasitism in wood ducks: a management dilemma. In Fredrickson LH, Burger GV, Havera SP, Graber DA, Kirby RE, Taylor TS, editors. Proc. 1988 North American Wood Duck Symposium. St. Louis (MO): The Symposium. p. 163–170.

Shaw RC, Hauber ME. 2009. Experimental support for the role of nest predation in the evolution of brood parasitism. J Evol Biol. 22: 1354–1358.

Shettleworth SJ. 2001. Animal cognition and animal behavior. Anim Behav. 61:277–286.

Soler JJ, Soler M, Pérez-Contreras T, Aragón S, Møller AP. 1999. Antagonistic antiparasite defenses: nest defense and egg rejection in the magpie host of the great spotted cuckoo. Behav Ecol. 10:707–713.

Stephens SE, Kaminski RM, Leopold BD, Gerard PD. 1998. Reproduction of wood ducks in large and small nest boxes. Wildl Soc Bull. 26:159–167.

Stevens JR, Wood JN, Hauser MD. 2007. When quantity trumps number: discrimination experiments in cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*). Anim Cogn. 10:429–437.

Sulkowski GM, Hauser MD. 2001. Can rhesus monkeys spontaneously subtract? Cognition. 79:239–262.

Thomson DL, Monaghan P, Furness RW. 1998. The demands of incubation and avian clutch size. Biol Rev. 73:293–304.

Trine CL. 2000. Effects of multiple parasitism on cowbird and wood thrush nesting success. In Smith JNM, Cook TL, Rothstein SI, Robinson SK, Sealy SG, editors. Ecology and management of cowbirds and their hosts. Austin (TX): University of Texas Press. p. 135–144.

Uller C, Jaeger R, Guidry G, Martin C. 2003. Salamanders (*Plethodon cinereus*) go for more: rudiments of number in a species of basal vertebrate. Anim Cogn. 6:105–112.

Washburn DA, Rumbaugh DM. 1991. Ordinal judgments of numerical symbols by Macaques (*Macaca mulatta*). Psychol Sci. 2:190–193.

West RE, Young RJ. 2002. Do domestic dogs show any evidence of being able to count? Anim Cogn. 5:183–186.

White DJ, Ho L, Freed-Brown G. 2009. Counting chicks before they hatch: female cowbirds can time readiness of a host nest for parasitism. Psychol Sci. 20:1140–1145.

Wynn K. 1992. Addition and subtraction by human infants. Nature. 358:749.