



Good prospects: high-resolution telemetry data suggests novel brood site selection behaviour in waterfowl

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ARTICLE INFO

Article history:

Received 12 December 2019

Initial acceptance 17 February 2020

Final acceptance 17 March 2020

MS. number: A19-00829R

Keywords:

brood habitat
brood prospecting
crowdsourcing
dabbling duck
electronic tracking
GPS
public information
site prospecting
Suisun Marsh

Breeding success should increase with prior knowledge of the surrounding environment, which is dependent upon an animal's ability to evaluate habitat. Prospecting for nesting locations and migratory stopover sites are well-established behaviours among bird species. We assessed whether three species of California dabbling ducks – mallards, *Anas platyrhynchos*, gadwall, *Mareca strepera*, and cinnamon teal, *Spatula cyanoptera* – in Suisun Marsh, California, U.S.A., a brackish marsh, prospect for suitable wetlands in the week prior to brooding. *K*-means cluster analyses grouped 29 mallard and gadwall hens into three groups. One group ($N = 13$) demonstrated evidence of brood site prospecting, with the fewest and latest prebrooding wetland visits. Of these hens, seven visited their future brood pond an average of 1.14 times and only shortly before brooding (1.29 days), obtaining current information on habitat suitability. For the remaining six hens, we did not detect a brooding wetland visit, possibly due to data limitations or because these hens acquired sufficient familiarity with the wetland habitat during nest breaks in adjacent wetlands, obviating the need to prospect the specific brood pond. The second identified group of hens ($N = 11$) visited the brooding wetland most frequently (on 4.55 days), further in advance (5.27 days), with the fewest unique wetland visits and the earliest brooding date (26 May). The final group of hens ($N = 5$) were the latest to brood (21 June) and visited the most wetlands, possibly due to less water or more broods present across the landscape. Brood ponds were always farther from the nest than the nearest ponds, indicating that habitat suitability or presence of conspecifics is more important to brood site selection. Prospecting provides hens with knowledge about current habitat conditions and allows them to 'crowdsource' public information regarding use of that habitat by other brooding hens. Prospecting may, therefore, benefit ducks inhabiting ephemeral habitats like those within Suisun Marsh, where brood habitat is limited and water cover changes rapidly during the breeding season.

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Understanding animal behaviour and describing behavioural strategies is critical to conserving and managing wildlife species (Festa-Bianchet & Apollonio, 2003). Variations in behaviour, such as individual responses to predation risk (e.g. López, Hawlena, Polo, Amo, & Martín, 2005; Mumma, Gillingham, Johnson, & Parker, 2017), reproductive strategies (e.g. Burger, Ryan, Dailey, & Kurzejeski, 1995) and foraging (Estes, Riedman, Staedler, Tinker, & Lyon, 2003; Kim, Tinker, Estes, & Koch, 2012), influence an animal's probability of survival and reproduction (i.e. fitness; reviewed

in Bolnick et al., 2003). These aspects of animal ecology are also affected by the habitat animals select for specific activities (Benson, Mills, & Patterson, 2015; King, Degraaf, Smith, & Buonaccorsi, 2006; McLoughlin, Dunford, & Boutin, 2005; Torgersen, Price, Li, & McIntosh, 1999). It follows that the choices animals make that influence their fitness depend upon their ability to evaluate habitat quality. For example, migratory taxa assess habitat quality based on factors such as vegetative structure, habitat composition (Saher & Schmiegelow, 2005), predation risk and forage availability (Ydenberg et al., 2002). They achieve this through direct sampling or prior knowledge of locations (see review in Moore & Aborn, 2000). Animals can also adjust breeding decisions according to local habitat conditions (Doligez et al., 2008). Thus, local individuals should attain knowledge of their surrounding habitat and track

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changes over time to make specific decisions to maximize fitness. Understanding this process is a critical facet of behavioural ecology (Stephens & Krebs, 1986).

Site prospecting is the behaviour through which individuals obtain knowledge of local conditions by investigating habitat and resource quality to determine its suitability for certain activities (Cox & Kesler, 2012; Scardamaglia, Fiorini, Kacelnik, & Reboreda, 2017; Valone & Templeton, 2002; Zicus & Hennes, 1989). Although this behaviour occurs in other taxa, including mammals, insects, reptiles and amphibians (Ponchon et al., 2013), it is most commonly described in bird species. In birds, prospecting behaviour has most often been related to the selection of migratory stopover points (Moore & Aborn, 2000) or future nest sites (Eadie & Gauthier, 1985; Reed, Boulinier, Danchin, & Oring, 1999). Performing this behaviour allows adults to meet energetic needs or reduce predation risk, thereby enhancing individual fitness and reproductive success (Ottosson, Bäckman, Smith, & Dickinson, 2001; Schjørring, Gregersen, & Bregnballe, 1999).

Ducks have been described prospecting for nest sites immediately before nesting (Bellrose & Kortright, 1976) and in the prior season (Eadie & Gauthier, 1985) to determine suitability of potential nesting sites through presence of still-incubating females or egg fragments. Studies suggest that site quality influences nesting or breeding success, and information gathered during nest site prospecting could lead to future nest success (Pärt, Arlt, Doligez, Low, & Qvarnström, 2011; Schjørring et al., 1999; but see Schuett, Laaksonen, & Laaksonen, 2012). If so, prospecting may be even more valuable in areas where suitable habitat is limited, heterogeneous or of low quality.

While prospecting for nesting locations and migratory stopover sites are well-established behaviours among bird species (Eadie & Gauthier, 1985; Moore & Aborn, 2000; Reed et al., 1999; Zicus & Hennes, 1989), prospecting for brood-rearing sites has not been documented. Effective brood habitats have specific requirements because, for example, predator densities can severely impact duckling survival (Ball, Gilmer, Cowardin, & Riechmann, 1975; Chouinard & Arnold, 2007; Mauser, Jarvis, & Gilmer, 1994). Therefore, the predation risk encountered during the traverse across inhospitable terrain from nest to brood pond should be minimized (Peterson et al., 2018). Additionally, suitable brood ponds for dabbling ducklings require forage (Kear, 1965; Korschgen et al., 1996; Nummi, Sjöberg, Pöysä, & Elmberg, 2000), low salinity (Mitcham & Wobeser, 1988; Swanson, Adomaitis, Lee, Serie, & Shoosmith, 1984) and vegetative cover to aid in predator avoidance (Chouinard & Arnold, 2007; Pearse; Ratti, 2004). The decision a successful nesting hen makes as to where to take her brood after hatch has significant implications for the potential success of that brood. In heterogeneous landscapes of ephemeral and unpredictable habitat, escorting broods to novel sites would seem to be a high-risk behaviour. Therefore, hens having knowledge of, or familiarity with, potential brood sites should be beneficial to brood success. It is likely that hens do not select brood sites at random but perform some kind of brood site selection prior to hatch, yet until now this has not been documented.

Brood-rearing sites may be selected through prior familiarity if suitable habitat is regularly used by hens during nest breaks. However, hens have different requirements during nest breaks and may not use the same ponds for brood rearing (Ringelman, Longcore, & Owen, 1982a; 1982b). If hens use different ponds for brood rearing and nest breaks, then they could obtain current information on the quality and suitability of nearby brood pond habitats by ‘prospecting’ as the hatch date approaches. If prospecting is a unique behavioural strategy, then nesting hens would likely first visit a brood pond closer to the time of hatch and would

visit that pond less frequently than birds that regularly used their brood pond for nest breaks.

California's Central Valley is a rapidly changing landscape that hosts large duck populations where habitat features (e.g. water coverage and pond quality) exhibit dramatic temporal variation. The Mediterranean climate, with dry, low rainfall summers, means that optimal summer breeding conditions for dabbling ducks are lacking (Central Valley Joint Venture, 2006; Chouinard & Arnold, 2007). In summer, few flooded ponds remain after the wet season ends, rainfall has halted and seasonal wetlands have been drawn down (Heitmeyer, Connelly, & Pederson, 1989), creating a seasonally heterogeneous, water-deficient environment that may be the cause of low mallard, *Anas platyrhynchos*, duckling survival rates (Mauser et al., 1994; Yarris, 1995). Suisun Marsh, on the eastern edge of the San Francisco Bay Estuary, is a brackish estuarine marsh that has areas of upland nesting fields and ponded water, affording a valuable opportunity to assess whether ducks exhibit brood site prospecting under circumstances where this behaviour could benefit site selection.

To determine whether dabbling duck hens in Suisun Marsh prospect for brood sites, we tracked them in the final stages of incubation with high-resolution GPS telemetry data (~5 m accuracy), which is helpful in identifying animal behaviour (Nathan & Giuggioli, 2013) and duck movement (McDuie et al., 2019). We explored relationships between selected brood ponds and the pattern of brood pond site use during nest breaks in the week leading up to hatching to identify different brood site selection strategies and address the following hypotheses.

(1) If dabbling duck hens in Suisun Marsh prospect for brood sites, then brood site selection strategies in the week prior to brooding should vary according to: (a) the number of times a hen visits the brood pond; (b) the number of days prior to brooding that the first visit to the brood pond occurs; (c) the number of unique habitat parcels (ponds) the hen visits; (d) the date that brooding begins.

(2) If brood site prospecting is a distinct behaviour from normal nest break behaviour, then the pattern of movement should reflect low numbers of visits to the brood pond prior to brooding and these visits should occur in the days nearest hatch to obtain the most current information on landscape and water coverage conditions.

(3) If hens try to minimize travel from the nest to the brood pond, brood ponds should be closer to the nest than to nest break ponds.

METHODS

Study Area

We tracked nesting hens of three species of California dabbling ducks – mallards, *A. platyrhynchos*, gadwall, *Mareca strepera*, and cinnamon teal, *Spatula cyanoptera*, at the Grizzly Island State Wildlife Area (~40.5 km² size; 38°09'N, 121°58'W) and surrounding private lands managed for waterfowl hunting in Suisun Marsh, California, U.S.A. (Fig. 1). Suisun Marsh is a 470 km² estuarine complex bordering the San Francisco Bay (described in Moyle, Manfree, & Fiedler, 2014) that experiences a Mediterranean climate, where rainfall is minimal to nonexistent during summer, and is dominated by managed wetlands. Levees divide the managed wetlands into ponds that are seasonally flooded and drawn down to promote growth of vegetation consumed by waterfowl (e.g. brass buttons, *Cotula coronopifolia*; sea purslane, *Sesuvium verrucosum*; alkali bulrush, *Scirpus maritimus*; swamp timothy, *Crypsis schoenoides*; Casazza, Coates, Miller, Overton, &



Figure 1. Map of Suisun Marsh and its position in California, U.S.A. Map shows the boundaries of all individual land parcels marked. Green parcels are independent hydrologic units in Suisun Marsh and vary in water content and levels throughout the year and across years. Yellow parcels are the established nesting fields where most of the mallard and gadwall hens in this study nested. Nests of the hens in this study (a small proportion of the total nests in Suisun) are indicated by red dots.

Yparraguirre, 2012; de Szalay & Resh, 1997; Miller, Burns, Wickland, & Eadie, 2009) and provide freshwater habitat during critical times of year. Grizzly Island State Wildlife Area also incorporates an upland area (~800 ha divided by roads and levees into 10–25 ha fields) intensively managed by the California Department of Fish and Wildlife to provide nesting habitat for ducks (Fig. 1). Most intensive nest searching occurred in this area and some additional nests were located in nearby isolated upland sections of seasonal wetlands.

Ethical Note

All capture and handling of ducks was carried out according to guidelines of the U.S. Geological Survey under the Western Ecological Research Center's Institutional Animal Care and Use Committee (WERC IACUC) and conducted under Federal Banding Permit No. 21142 and state Scientific Collecting permit No. SC-8090. Hens were flushed without injury from nests located using

standard nest-dragging techniques (McLandress, Yarris, Perkins, Connelly, & Raveling, 1996); in short, a 50 m rope, incorporating rock-filled cans that create noise, are dragged approximately 0.5–1 m above nests between two all-terrain vehicles across upland nesting fields. Nest locations were marked with GPS and a bamboo flag. Eggs from each nest were candled to determine embryo development and expected hatch date (Weller, 1956) and, following a minimum of 8 days of incubation, hens were then captured using either a long-handled net or a funnel trap placed on the nest. Funnel traps are checked approximately 3–4 h after placement to allow time for the hen to return to the nest undisturbed. Hens were marked with individually numbered aluminium leg bands (29 of 30 individuals; 1 recapture), aged as second year (SY; subadults), after second year (ASY; adults) or, if this could not be distinguished, after-hatch-year (AHY) based on feather and moult plumage (Carney, 1992), and measured for standard morphometrics (e.g. mass, culmen length) to ensure GPS-GSM transmitter deployment weight was not greater than 1–3% of body mass

(Kessler et al., 2014; Phillips, Xavier, Croxall, & Burger, 2003) for any captured individual. Handling time averaged 15 min and never exceeded 30 min per individual, after which they were released at the location of capture. No birds were injured or suffered long-term effects of transmitter deployment during this study.

Electronic Tracking and Data Analysis

Between April and July 2015–2018, we fitted hens with remotely programmable Ecotone GPS–GSM SAKER L transmitters (Ecotone Telemetry, Gdynia, Poland), and in 2018, we used Ornitela Ornitrack 15 transmitters (Ornitela, Vilnius, Lithuania). Transmitters incorporate a miniaturized solar panel to allow charging while deployed and transmit position location data (e.g. coordinates, date, time) via cellular text message on the GSM network. Transmitters were epoxied to a small foam pad and attached to the backs of captured birds with harnesses made of 5 mm automotive elastic, which minimizes wicking of moisture to down feathers while minimizing impairment of normal movement and flight (Ecotone transmitters: deployment size: $58 \times 27 \times 18$ mm, deployment weight: 17 g; deployment size: $40 \times 25 \times 19$ mm, deployment weight: 14 g; Ornitela transmitters: deployment size: $58 \times 25 \times 14$ mm, deployment weight: 16 g).

Time intervals at which transmitters obtained locations varied depending on battery life from 30 to 360 min. At the lowest interval (4 locations/day) there was a chance we would not capture a nest break by a hen and as a result, prospecting or prior visits to the brood pond may have been missed. However, to minimize the chance of missing a nest break when prospecting may occur, we programmed the transmitters to collect GPS locations at times (local time 0500, 1100, 1700 and 2300 hours) to match known mallard and gadwall nest recesses (nest recess start times ~ 0615 and 1630 hours; Croston et al., 2020) at our study site. Mallards, average 1.7 nest breaks/day and remain away for an average 106 min in the morning and 155 min in the afternoon (~1630–1900 hours). Gadwall by comparison, average 1.4 nest breaks/day of 91 min (morning) and 193 min (afternoon; 1630–1940 hours). Birds that took only a single nest break were most likely to do so in the afternoon (Croston et al., 2020). Therefore, we believe that, even at the minimum frequency of four GPS locations/day, we optimized our chance of capturing at least one nest break per day for each individual to detect the behaviour of interest (brood site prospecting).

Nests were visited immediately following the expected hatch date to determine their overall fate (i.e. hatched, abandoned, depredated) and the number of eggs that hatched. We only used data from hens with nests that hatched and had a minimum of 7 days of tracking prior to hatch so that nest break patterns could be reliably assessed. We required 7 days of data after the hen and brood departed from the nest to capture brooding behaviour. Birds were classified as brooding if their movements following a successful nest hatch were indicative of travelling with ducklings (i.e. speed < 5 km/h, relatively linear travel to suitable brooding habitat). We defined the start of the brooding period as the first location received away from the nest following a successful hatch and considered brooding to be over (i.e. offspring successfully fledged or brood failed) when the hen violated the travel speed condition above or departed from a location and remained away for more than 2 h (Rotella & Ratti, 1992).

Parcels were manually classified to produce a map of ponded water across Suisun. Based upon visual interpretation of LiDAR elevation data and satellite orthoimagery, we identified property or physical boundaries (e.g. levees, dikes, roads) and digitized hydrological units (Fig. 1). We downloaded cloud-free RapidEye multispectral satellite data from the Planet Open California Data

portal imagery (Planet Team, 2018) for each year, as close to 15 June as possible, which we estimated to be the date when most ducklings are on the landscape based on nest initiation dates for mallards in California (McLandress et al., 1996). In ArcGIS 10.5.1 (Environmental Systems Research Institute (ESRI), Redlands, CA, U.S.A.), we visually interpreted the satellite imagery and classified the parcels for each year as wet (water visible) or dry (no water visible). In some instances, only portions of the parcel were wet, and in these cases these areas were given separate boundaries. The classifications were validated by landowners and experts familiar with the parcels. GPS locations in the dry upland parcels were excluded because the habitat is unsuitable for ducklings and offers no potential for use as brood habitat. For nests in wet parcels, we eliminated all locations within a 20 m buffer around the nest to account for GPS error and locations resulting from hens that had been flushed off the nest from study site disturbance.

To understand and assess nest break/brooding activity, each GPS location was spatially joined to the parcel ID and the wet/dry classification into which it fell using the Simple Features package in R v.3.5.3 (Pebesma, 2018). To account for GPS error, all points were also joined to adjacent ponds within a 10 m buffer of the location. Our aim was to identify which ponds each hen visited each day. Any visit could be represented by one or more locations, and/or one or more visits within a day due to variability in location frequency within and among individuals. Therefore, all ponds used were counted once per day, regardless of the number of locations within. Habitat conditions within a single pond (e.g. water level, vegetative cover, etc., bound by levees and canals) are generally relatively homogenous compared with differences across ponds.

We used time to first brooding location rather than time to nest hatch, because there is evidence that hens will keep ducklings in the nest for 1–2 days following hatch (Peterson et al., 2018). We visually assessed the movement tracks of hens following hatch to identify the pond location to which each hen brought her brood. To determine whether brood site prospecting exists as a separate activity from the bird's normal nest break behaviour, we quantified the frequency and temporal pattern of visits to the specific pond used for brooding during the week prior to nest departure, with respect to the number of visits and when the first visit to that pond occurred (see Results, Fig. 2). To determine whether hens selected the closest possible habitat (pond) for nest breaks or brooding, we calculated distances from each hen's nest to (1) the nearest pond that could potentially be used for nest breaks or brooding, (2) all nest break locations (which were then averaged by individual) and

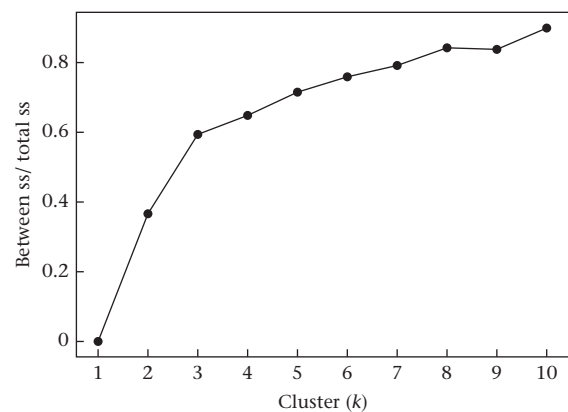


Figure 2. Sum of squares (ss) analysis to assess the optimal number of clusters for K-means clustering analysis of dabbling duck hens of Suisun Marsh. The line that divides the between sum of squares by the total sum of squares begins to asymptote at three clusters.

(3) the brood pond. The nearest pond distance was measured from the nest to the edge of the closest wet area that was not a channel. Distance to nest breaks was measured as the average distance to all locations that each individual hen used for nest breaks by day, and then averaged across the week prior to hatching. Brood pond distance was measured as the distance from the nest to the first GPS location in the identified brood pond. Distances were calculated using the Euclidean distance tool in ArcGIS 10.5.1.

Statistical Analyses

All statistical analyses were completed in R v.3.5.3 (R Core Team, 2019). To determine whether GPS location frequency affected our ability to identify nest breaks, we compared the total number of GPS locations obtained for each individual by behaviour with a Kruskal–Wallis test and Holm–Sidak or Dunn’s method for pairwise comparisons. To identify divergence in behavioural strategies for nesting hens and whether prospecting is a unique brooding strategy, we performed a *K*-means cluster analysis (Forgey, 1965; Hartigan & Wong, 1979; Lloyd, 1982; MacQueen, 1967) on our data to objectively determine how many behavioural strategies would be identified by individual cluster groupings (R Core Team, 2019). From our data we selected four factors to be used in the cluster analysis: the Julian date of when brooding began; the number of unique wetland units the hens visited in the week prior to brood rearing; the total number of visits to the brood pond in the week prior to brood rearing; and finally, when the first visit to the brood pond occurred (measured in terms of number of days in advance of leaving the nest). Analyses of the sum of squares (SS) and silhouette plots (Rousseeuw, 1987) were used to determine the number of clusters (Fig. 2).

We compared the distance to the nearest pond and the distance to both the average nest break distances travelled and the distance to the brood pond across all hens regardless of cluster with Mann–Whitney rank-sum tests using the R statistical package (R Core Team, 2019). To ensure variance in the amount of data collected from each individual did not affect results, we tested the differences among clusters in the numbers of GPS locations obtained from each hen overall and over the final 7 days with Kruskal–Wallis one-way ANOVAs with Dunn’s multiple pairwise comparisons. To determine whether the amount of data we collected varied among clusters, we tested the numbers of days during which no GPS locations were obtained for hens in parcels away from their nest (i.e. on nest break) with a one-way ANOVA. Finally, we tested for differences in hen age among clusters with a Fisher’s exact test using the R statistical package (R Core Team, 2019). One hen of indeterminate age (AHY) was excluded from this analysis. All results are presented as mean \pm 1 SE unless otherwise noted.

RESULTS

There were 29 hens (20 mallard, 7 gadwall, 2 cinnamon teal) that met our criteria to test brood site prospecting (Table 1). Based on the analysis of the sum of squares, we determined that these 29 tracked hens were best grouped into three clusters for the *K*-means cluster analysis (Fig. 2).

Cluster 1 consisted of 13 individuals (9 mallard, 4 gadwall) that had the fewest visits to the pond that they ultimately used for brooding (the brood pond – the first pond to which the hens took their broods after hatching) and the latest first visit to the brood pond (measured as number of days prior to nest departure; Table 2). Six of these 13 hens never previously visited the brood pond, shown by negative values for the number of days prior to brooding of the first brood pond visit in Table 1. The negative values

represent the number of days after hatch that the first visit to that brood pond occurred; e.g. 0 reflects a visit on the day of hatching, -1 reflects a visit on the day following hatching. Of the other seven hens in cluster 1, six visited the brood pond on 1 day and one hen visited on 2 days. Brooding for this group was initiated around the peak hatch time for Suisun Marsh breeding ducks, with an average brood date of 29 May (most hatching in California occurs in late April through late June and peaks in mid-May; McLandress et al., 1996).

Cluster 2, with 11 tracked hens (7 mallards, 2 gadwall, 2 cinnamon teal), visited the fewest unique parcels, had the earliest brood initiation date (25 May) and the earliest first visit to the brood pond, which they visited on more days than the other clusters (Table 2). Finally, cluster 3 was composed of only five hens, which visited the most unique parcels, and the onset of brooding occurred later in the season (21 June) than for the other clusters (Table 2). The hens in this cluster visited their brood pond almost as often as hens in cluster 2 and their first visit was almost as many days prior to brooding (Table 2).

When comparing distances, all hens used nest break ponds (mean distance to all nest break locations: $\bar{X} \pm SE = 953.3 \pm 150.2$ m; Mann–Whitney *U* test: $U = 240.0$, $N_1 = N_2 = 29$, $P < 0.01$; Table 1, Fig. 3) and brood ponds ($\bar{X} \pm SE = 976.4 \pm 112.4$ m; $U = 159$, $N_1 = N_2 = 29$, $P < 0.001$; Table 1, Fig. 3) that were significantly farther from their nest than the nearest pond ($\bar{X} \pm SE = 376.7 \pm 54.0$ m, $N = 29$) that could potentially be used for either activity.

There were no significant differences between clusters in the number of days during which no locations were obtained of hens in parcels away from their nest (i.e. on nest break) in the week prior to hatch (Kruskal–Wallis test: $H_2 = 4.326$, $P = 0.115$; $\bar{X} \pm SE$: cluster 1: 1.7 ± 0.3 days, $N = 13$; cluster 2: 1.1 ± 0.4 days, $N = 11$; cluster 3: 0.2 ± 0.2 days, $N = 5$). In addition, the number of days during which no locations were obtained for the hens in cluster 1 that never visited the brood pond did not differ ($\bar{X} \pm SE = 1.5 \pm 0.6$ days, $N = 6$) from that of the other hens in cluster 1 ($\bar{X} \pm SE = 1.3 \pm 0.4$ days, $N = 7$) or from that of clusters 2 and 3 (ANOVA: $F_{3,25} = 1.334$, $P = 0.286$). Analysis of hen age by cluster using a Fisher’s exact test revealed no evidence of a relationship between hen age and behavioural clusters ($P = 0.53$).

DISCUSSION

Most of our tracked hens (23/29; 79.3%) brought their broods to ponds they had previously visited during incubation, while a prior visit to the future wetland brooding site was never detected in the 7 days prior to duckling hatching for the remaining six hens. In all cases the brood pond was farther away from the nest than the nearest possible pond that may have potentially been used for brooding. The six hens that never visited the brood pond were clustered (cluster 1) with another seven hens that ‘prospected’ their future brood pond, visiting infrequently (only once or twice), shortly before their ducklings hatched (maximum of 3 days prior; see Fig. 4a for example). Site prospecting during the latter stages of incubation can increase the hens’ breadth of knowledge about the landscape, allowing them to locate a pond with suitable brood habitat, particularly if they had been using suboptimal brood sites for nest breaks. Pond drainage (draw down) occurs throughout spring and summer, and satisfactory ponds can become unsuitable for ducklings within 1–2 days (Central Valley Joint Venture, 2006; USBR, 2013). As draw down progresses, water recedes from the vegetated edges and collects in the centre, resulting in higher pond salinity and less flooded, emergent vegetation that hens and ducklings can use for cover. Dabbling ducklings can only tolerate low salinity conditions (Mitcham & Wobeser, 1988; Swanson et al.,

Table 1
Late-stage nesting data for three clustered groupings of dabbling duck hens in Suisun Marsh showing the numbers of GPS locations per individual, GPS locations per day, GPS locations on nest breaks and the number of GPS locations excluded (from dry upland fields or nest buffers) as well as the four factors used in *K*-means clustering analyses to identify the three clusters of hens

Hen ID	Species	Total no. of GPS locs	Avg. GPS locs/day	Total no. of nest break locs	No. of GPS locs excluded	Brood initiation	Unique wetland units	Total brood pond visits	No. of days prior to brooding of 1st brood pond visit	Age	Distance to nearest pond (m)	Mean distance to nest break ponds (m)	Distance to brood pond (m)	Cluster
180650.1	Gadwall	44	6.3	8	36	3 June	2	1	1	SY	901.9	1490.4	1720.5	1
BIRD 02.1	Mallard	24	4	7	17	18 May	3	0	0	ASY	263.3	738.6	1606.7	1
BIRD 09.1	Mallard	155	22.1	35	120	18 May	3	0	-1	SY	587.8	2386.0	2030.9	1
BIRD 13.1	Mallard	74	10.6	36	38	18 May	3	0	-2	ASY	712.2	132.8	1413.4	1
BIRD 14.1	Mallard	48	8	12	36	25 May	2	1	3	ASY	804.5	2012.3	1305.5	1
BIRD 21.1	Mallard	121	17.3	19	102	25 May	4	1	0	ASY	411.0	2647.9	824.7	1
BIRD 26.1	Gadwall	58	9.7	10	48	2 June	4	2	2	ASY	287.5	1249.5	613.2	1
BIRD 33.1	Mallard	40	5.7	24	16	23 June	6	0	0	SY	98.4	309.9	1537.6	1
BIRD 45.1	Mallard	53	7.6	11	42	11 June	7	1	2	ASY	95.1	456.0	519.8	1
DRIB 13.2	Mallard	81	11.6	21	60	23 May	2	1	0	SY	255.0	420.5	422	1
DRIB 58.1	Gadwall	25	3.6	9	16	5 July	1	0	-1	SY	159.6	37.2	491.6	1
SAKR 17.2	Mallard	81	11.6	12	69	5 May	3	0	-1	SY	77.5	795.8	1495.7	1
WATE 05.1	Gadwall	235	33.6	6	229	1 June	5	1	1	ASY	659.7	1874.8	1718.9	1
180615.1	Mallard	85	12.1	10	75	1 June	3	4	5	ASY	706.3	1588.1	1580.9	2
180651.1	Mallard	101	14.4	33	68	11 June	2	6	5	SY	263.9	461.0	569.5	2
BIRD 15.1	Gadwall	74	10.6	5	69	22 May	2	5	6	ASY	755.2	2418.9	2391.9	2
BIRD 17.1	Mallard	57	11.4	5	52	24 May	2	3	4	AHY	154.6	250.1	425.4	2
BIRD 24.1	Mallard	74	10.6	23	51	27 May	4	2	6	ASY	472.6	1444.9	697.4	2
DRIB 29.2	Gadwall	61	8.7	30	31	24 May	1	6	6	ASY	91.0	95.8	179.9	2
DRIB 53.1	C. teal	59	11.8	38	21	24 May	3	1	6	ASY	704.2	227.0	1018	2
TEAL 49.1	C. teal	67	11.2	41	26	5 June	2	6	5	ASY	16.2	115.1	344	2
WATE 64.2	Mallard	79	11.3	37	42	21 May	5	7	6	ASY	118.4	969.0	212.7	2
WATE 72.2	Mallard	272	38.9	143	129	6 May	7	6	6	ASY	4.8	200.3	380.3	2
WATE 81.2	Mallard	81	11.6	19	62	23 May	5	4	3	ASY	451.3	830.8	972.1	2
180619.1	Gadwall	92	13.1	49	43	25 June	11	3	2	ASY	953.9	2027.4	1294.7	3
BIRD 40.1	Mallard	197	28.1	90	107	3 June	10	7	6	ASY	210.9	710.5	754.9	3
SAKR 03.1	Mallard	130	21.7	80	50	4 July	9	1	3	ASY	112.0	235.8	1097.5	3
SAKR 19.1	Mallard	161	23	79	82	11 July	7	7	6	ASY	151.9	196.2	299	3
WATE 04.1	Mallard	317	45.3	35	282	2 June	9	3	6	ASY	443.6	1322.3	396.9	3

SY: second year; ASY: after second year; AHY: after hatch year.

Table 2
Summary results from *K*-means cluster analysis showing the average results for all four factors used in the cluster analysis to separate hens into clusters 1–3 by behaviour; i.e. the date that brooding was initiated, the day prior to brooding that the first visit to the brood pond occurred, the numbers of unique wetland units (ponds) visits and the total number of times the hens visited the brood pond

Cluster	<i>N</i>	Brood initiation date	Day of 1st visit	Unique parcels	Total visits
1	13	29 May (± 8.6 days)	0.31 \pm 0.87	3.46 \pm 1.04	0.62 \pm 0.39
2	11	25 May (± 6.2 days)	5.27 \pm 0.68	3.27 \pm 1.21	4.55 \pm 1.29
3	5	21 Jun (± 22.1 days)	4.6 \pm 2.42	9.2 \pm 1.84	4.2 \pm 3.33

N is the number of hens ascribed to each cluster. Values are means \pm SE.

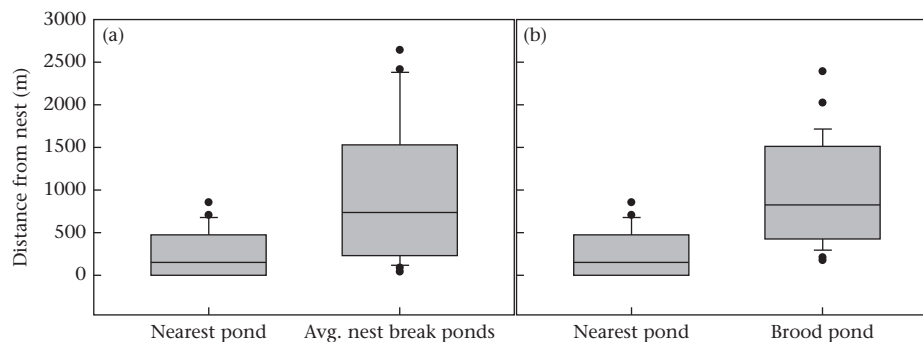


Figure 3. (a) Distance from dabbling duck nests to the nearest pond and average distance travelled from dabbling duck nests to nest break ponds during the week prior to hatching. (b) Distance from dabbling duck nests to the nearest pond and the brood pond. The ends of the boxes define the 25th and 75th percentiles, with a line at the median and error bars defining the 10th and 90th percentiles. Circles are outliers.

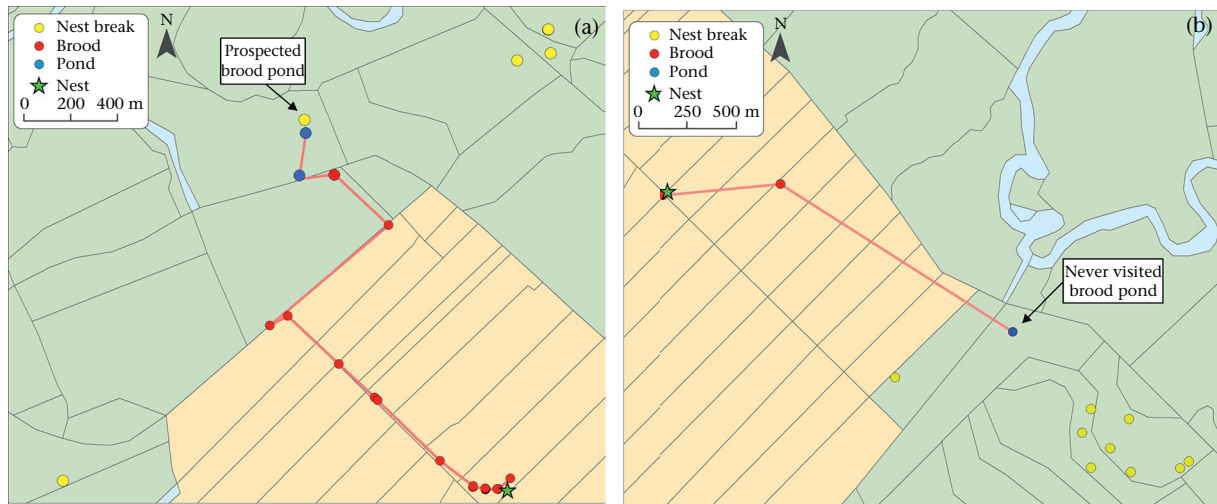


Figure 4. Nest to brood pond tracks of dabbling ducks. Example of the incubation and posthatching behavioural strategies of two Suisun breeding hens from cluster 1. The yellow dots represent nest breaks. Nest breaks that consisted of more than one GPS location are collapsed to single yellow dots for illustrative clarity. The red dots and tracks show the paths taken by the hens and their ducklings from the nests (green star) to the brood pond (which is indicated by the blue dot/s). (a) An example of a hen that prospected the brood pond on only one single day prior to taking her brood to that pond. (b) An example of a hen that took her brood to a pond that she had never previously visited but that was adjacent and/or en route to the ponds that she had used for regular nest breaks in the week prior.

1984), and the amount of vegetated wetland is positively related to duckling survival (Simpson, Yerkes, Nudds, & Smith, 2007), so reduced water substantially increases duckling mortality (Krapu, Pietz, Brandt, & Cox, 2006). Therefore, a single visit to the brood pond, closer to the time of the ducklings hatching, may be sufficient for the hen to determine whether the pond is suitable.

Brood habitat suitability is not limited to pond features and habitat quality; the pond must also be within the travel distance limits of ducklings. However, the relationship between duckling survival and distance travelled to the first brood wetland is variable. Some studies found no relationship between duckling survival and distance travelled to the first brood wetland (Dzus & Clark, 1997; Guyn & Clark, 1999), others demonstrated an inverse relationship between distance moved and survival (Rotella & Ratti, 1992; Simpson et al., 2007) and yet others demonstrated a positive relationship (Davis, Cox, Kaminski, & Leopold, 2007). The danger of overland travel from nest to pond (Chouinard & Arnold, 2007; Mauser et al., 1994) is likely related to increased predator interactions, which, unsurprisingly, negatively affect duckling survival (Amundson & Arnold, 2011; Grenfell, 1978; Pearse; Ratti, 2004). In Suisun, hens and broods can reduce overland travel by using waterways, but river otters, *Lutra canadensis*, that inhabit these ditches and sloughs are known to depredate waterfowl and ducklings (Grenfell, 1978; Talent, Jarvis, & Krapu, 1983). Consequently, hens that use nest break sites that are too far from the nest for ducklings to travel may benefit from prospecting for suitable ponds that are closer to the nest to minimize travel distances.

Interestingly, the clustering of prospecting hens with hens that never visited the brood pond implies that either 'zero visits' is a real finding and clustering was based on other behavioural traits (date, number of ponds visited), or zero-visit hens are prospecting hens but data limitations caused us to miss prior brood pond visits. If so, the implications would be that zero-visit hens may in fact be prospectors, or that prospecting hens should be redefined as having visited more frequently. However, as the average number of days on which no data were collected for hens while on nest breaks did not vary among our clusters, and the zero-visit hens did not have fewer days of data than any other group, this is unlikely to explain the differences we observed.

These hens may have obtained current pond condition information some other way. For example, a hen may have ultimately taken her brood to a pond either en route or adjacent to the pond used for regular nest breaks. This would have precluded the need for an actual visit to the pond (see Fig. 4b for an example of this behaviour). Alternatively, another environmental cue that may influence brood site selection is the presence of other individuals. Dabbling ducks are very social and have pronounced flocking behaviour and even tend to foster the young of other ducks through brood amalgamation (Beauchamp, 1997, 1998; Eadie, Kehoe, & Nudds, 1988). Unfortunately, we did not have sufficient data on broods across the landscape at the time these hens were brooding to determine whether this factor influenced brood site selection by the hens in our study. However, the use of public information, where individuals in social groups can observe the behaviour of conspecifics and improve their estimation of the surrounding environment, is a recognized phenomenon in behavioural ecology (Doligez, Danchin, & Clobert, 2002; Pärt & Doligez, 2003; Valone & Templeton, 2002). Birds are known to derive information about reproductive success by inspecting feeding rates or offspring quantity (Calabuig, Ortego, Aparicio, & Cordero, 2010; Doligez et al., 2002; Pärt & Doligez, 2003). This 'crowdsourcing' behaviour can inform individuals about the success of conspecifics and allow them to key in on those areas when selecting future breeding sites. Therefore, crowdsourcing public information can benefit individuals by reducing uncertainty and the time required to estimate habitat quality (Valone & Templeton, 2002) and improve reproductive success.

Within our data, three other hens (from clusters 2 and 3) exhibited at least one of the behaviours characteristic of brood site prospecting. All three only visited the brood pond once or twice, but two of these hens (in cluster 2) visited a week before brooding, which violates our assumption that prospecting should provide current pond information. As conditions in marsh ponds can change within a day or two, information about whether the habitat will be suitable for those hens and their ducklings by the time brooding commences is less likely to be accurate. The third hen (in cluster 3) only visited her brood pond once and the visit occurred 3 days prior to brooding. This time frame is slightly farther out than the other hens that showed evidence of prospecting but may be

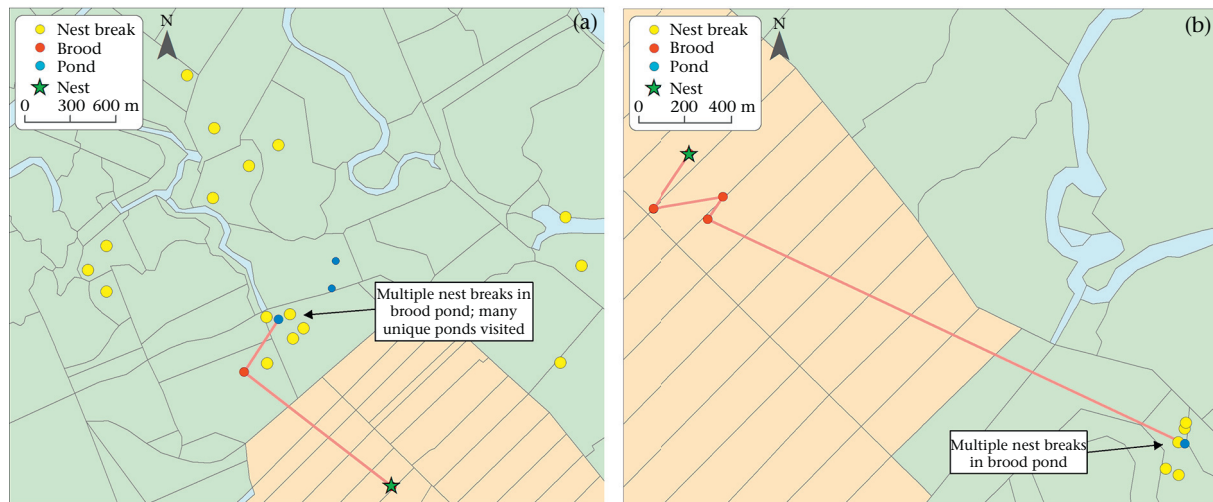


Figure 5. Nest to brood pond tracks of dabbling ducks. Example of the incubation and posthatching behavioural strategies of two Suisun breeding hens. The yellow dots represent nest breaks (multiple locations are collapsed to a single point for illustrative clarity). The red dots and tracks show the paths taken by the hens and their ducklings from the nests (green star) to the brood pond (blue dot/s). (a) An example of a hen from cluster 3. These individuals were behaviourally similar to the hens from cluster 2 insofar as they used regular nest break ponds for brooding but, as indicated by the more numerous yellow nest break dots, they explored more unique ponds prior to brooding and did so much later in the season. (b) An example of a hen from cluster 2 that used regular nest break ponds as the brood pond.

near enough that pond condition information would be reliable. This hen was most likely grouped into cluster 3 due to brooding later in the season and showing the same propensity to visit more new ponds in the days leading up to hatch as the other four birds in cluster 3 (Fig. 5a). This strategy may be related to experience, as later breeding coincides with more challenging conditions including higher ambient temperatures, which affect egg survival, and reduced habitat and water levels across the landscape (Central Valley Joint Venture, 2006; De Andrade, Rogler, & Featherston, 1976; Oguntunji; Alabi, 2010; USBR, 2013). Unfortunately, we were unable to comprehensively assess a relationship between hen experience and brood timing due to very low recapture rates of banded hens in this system. However, although we found no significant difference in the ages of hens in our clusters, cluster 3 consisted only of adult (ASY) birds, which could be explained by adult ducks being 1.5× more likely to renest later in the season than younger (SY) hens (Arnold, Devries, & Howter, 2010). The hens in this cluster may have gleaned information about optimal brood habitat by visiting more ponds and observing the presence of other broods. This would be especially relevant later in the season, after peak nest hatching, when brood density is maximized, and is a theory that should be addressed in future research.

The final group of hens (cluster 2) exhibited a different strategy whereby they took their broods to a pond they had regularly used for nest breaks over the preceding week (Fig. 5b). These hens nested/brooded the earliest and explored the fewest ponds, which may imply a level of experience through which they can select optimal nest break sites that offer appropriate habitat for both themselves and their ducklings, eliminating the need to search for better brood ponds due to a greater amount of suitable pond habitat within the marsh earlier in the season. In addition, the amount of public information available to the hen on the landscape would be minimal as few young would be present on the landscape during this earlier time period.

Conclusion

Prospecting has been cited as the process of information gathering about the suitability of a region or site for nesting in breeding

birds (Eadie & Gauthier, 1985; Reed et al., 1999). Hens must ensure the habitat to which they take their brood provides the best opportunity of successfully raising and fledging their ducklings, and this study provides the first evidence of this strategy being used in brood site selection. Brood ponds were consistently farther from the nest than the nearest available pond, suggesting that habitat suitability and/or presence of other broods are more important considerations for brood rearing. Moving farther from the nesting area may be an avoidance strategy used to confuse predators, and future research might investigate this hypothesis through combined duckling and predator tracking. Hens adopted a variety of dispersal strategies to locate better-quality or more suitable habitat. However, whether they primarily cued in on habitat features or the presence of conspecifics or other dabbling duck species is unclear. Understanding the relationship between habitat quality and brood site selection and use could be accomplished with accurate data on environmental characteristics such as pond size, salinity, amount of open water, percentage of vegetative cover, seed loads, etc., which are currently being developed. Additionally, to understand how important crowdsourcing behaviour is in providing public information about site quality, or whether a hen's experience contributes to brood site selection, future research should attempt comprehensive concurrent tracking of hens and ducklings and assess hen experience through mark–recapture. By combining these data, we could then quantify the relationship between brood success, experience and prospecting behaviour, and how habitat features and environmental characteristics affect brood site selection strategies in waterfowl.

Acknowledgments

We thank the following for contributions to the completion of this research: field work, capture, trapping, handling and tagging of ducks was completed by Katharine Cody, Breanne Cooney, Alex Dopkin, Daniel Essert, Matthew Falcon Brady Fettig, Katharine Fielding, Michael Fontana, Jacob Gray, Andy Greenawalt, Rich Hansen, Clint Helms, Melissa Hunt, Jeffrey Kohl, Nathan LaShomb, Desmond Mackell, Elliott Matchett, Andrea Mott, Matthew Prinzing and Ivonne Romero. We thank the Grizzly Island State Wildlife Area and California Department of Fish and Wildlife staff for assistance

with all aspects of the field data collection including collection including Patrick Graham, Orlando Rocha and Shawn Overton. We also thank the staff of the Suisun Resource Conservation District for their logistical assistance including Steve Chappell, John Takekawa, Bruce Wickland, Jeff Taylor, Tim Edmunds and Dean Podolsky. Lisa Parker provided administrative support. We thank Brian Davis and an anonymous referee for their helpful comments and recommendations to improve this manuscript. Funding for this study was provided by the California Department of Water Resources and the U.S. Geological Survey. The data sets used and analysed are available from the corresponding author on reasonable request. M.C., C.F. and J.A. conceived the original idea, design and experiment. M.C. and F.M. authored the manuscript with input from all authors. C.O. provided the data set. F.M. and D.K. processed the data, and analyses were conducted by D.K., F.M., A.L. and J.Y. C.F. contributed substantial resources and funding. We declare no conflicts of interest. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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