Behav Ecol Sociobiol (2017) 71:23
DOI 10.1007/s00265-016-2250-8

ORIGINAL ARTICLE

Planning host exploitation through prospecting visits by parasitic cowbirds

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Received: 17 August 2016 / Revised: 22 November 2016 / Accepted: 24 November 2016

Abstract
We studied visits to potential host nests by two avian brood parasites, the host generalist shiny cowbird, *Molothrus bonariensis*, and the host specialist screaming cowbird, *Molothrus rufoaxillaris*, in the periods preceding and overlapping the laying period of their hosts. Our goal was to examine the hypothesis that during prelaying visits, cowbird females form a dynamic memory library of laying opportunities, which they deploy to target suitable nests at a later predawn period. We recorded presence of radio-tagged females within a fixed area around nests of chalked-browed mockingbirds, *Mimus saturninus* (a common host of shiny cowbirds), and baywings, *Agelaioides badius* (the main host of screaming cowbirds), using proximity data loggers placed at nests during prelaying, laying and early incubation. Our data confirmed that females of both species visit potential host nests prior to laying and that parasitic events occurred before dawn, earlier in screaming than shiny cowbirds but with little chance of host nests having been discovered on the laying day. There were interesting species differences: visits were less frequent in shiny than screaming cowbirds and the former rarely returned after laying, while screaming cowbirds visited nests repeatedly after laying and occasionally showed repeat parasitism. The higher frequency of revisiting by screaming cowbirds to baywing nests is consistent with the uncommonly long and variable baywing prelaying period, and the incidence of repeat parasitism may reflect low availability of baywing nests and greater flexibility of its parental care potential thanks to it being a social breeder.

Significance statement
Avian brood parasites synchronize their laying with that of their hosts, as this reduces egg rejection and optimizes hatching time. They also avoid parasitizing nests repeatedly, thus preventing harm to their own previously laid eggs and competition among their offspring. Further, they lay at dawn, so that location of target nests must be known from previous days' exploration. It has been argued that these adaptations must depend on memory for the location and status of host nests within their home range, a memory feat known as 'bookkeeping'. We study nest prospecting in a host specialist and a host generalist parasitic cowbird, using a combination of proximity radio tracking and video recordings. Our results confirm the prospecting hypothesis, report previously unknown interspecies differences and illustrate how cognitive adaptations can be studied in the context of field behavioural ecology.

Keywords Brood parasitism · *Molothrus bonariensis* · *Molothrus rufoaxillaris* · Nest searching · Automated telemetry

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Communicated by M. Soler

Electronic supplementary material The online version of this article (doi:10.1007/s00265-016-2250-8) contains supplementary material, which is available to authorized users.

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Introduction

The decision about where to breed is a fundamental determinant of success for many species, and potential breeders benefit by gathering information about potential sites before making a choice (Doligez et al. 1999; Seeley and Buhrman 2001; Arlt and Pärt 2008; Selonen and Hanski 2010). Such prospecting behaviour is important for an organism's fitness and particularly interesting in parasitic species that gather information on their potential hosts' breeding sites and/or status before choosing where to lay their eggs. The parasitoid wasp *Hyposoter horticola*, for example, locates host egg clusters in the weeks before the hosts become vulnerable to parasitism and later returns to parasitize them (Van Nouhuys and Ehrnsten 2004). In two intraspecific brood parasitic ducks, Barrow's Goldeneye (*Bucephala islandica*) and Common Goldeneye (*Bucephala clangula*), females prospect for nesting sites at the end of the breeding season, and nest sites that are visited more frequently by prospecting females in one year have a higher probability of being parasitized in the next year (Pöysä 2006).

Interspecific avian brood parasites such as cuckoos and cowbirds lay their eggs in nests of other species, the hosts, which provide parental care for parasite's eggs and chicks (Rothstein and Robinson 1998; Davies 2000; Spottiswoode et al. 2012). This reproductive strategy frequently involves that parasitic females search for host nests in which to lay their eggs (Wiley 1988; Honza et al. 2002; Soler and Pérez-Contreras 2012) and then remember their location, so as to return at the time of laying. Host nest's status at the time of laying is typically aimed at the laying period of the host (Fiorini and Reboreda 2006; Moskát et al. 2006), as this maximizes parasite's hatching success and chick survival (Fiorini et al. 2009; Soler et al. 2015).

Female cowbirds search for nests within relatively constant areas throughout the breeding season (Hahn et al. 1999; Scardamaglia and Reboreda 2014). They may locate host nests using environmental features related to nest placement (Clotfelter 1998), host activity during nest building (Wiley 1988; Kattan 1997; Banks and Martin 2001; Robinson and Robinson 2001) or nest defence responses by hosts directed towards them (Robertson and Norman 1976, 1977; Smith et al. 1984) or to other parasite females (Gloag et al. 2013). Cowbird females do return to parasitize nests mainly during host laying (Mermoz and Reboreda 1999; Astié and Reboreda 2009). They lay mostly around dawn (Scott 1991; Peer and Sealy 1999; Gloag et al. 2013), and at the time of laying, they fly directly from their roost to a target nest, which is typically located within the area that the female visited on previous days (Scardamaglia and Reboreda 2014), suggesting that they know the location of target nests through their previous prospecting of the area.

There is evidence that at least in some species of cowbirds (brown-headed cowbird, *Molothrus ater*: Alderson et al. 1999; McLaren et al. 2003; Ellison et al. 2006; shiny cowbird, *Molothrus bonariensis*: Gloag et al. 2014), females rarely return to lay eggs in nests that they have already parasitized (but see Rivers et al. 2012; Rivers and Peer 2016). This avoidance of repeated parasitism may serve to reduce competition among a female's own offspring and since they remove or puncture both hosts and cowbirds' eggs on laying visits (Fraga 1998; Peer 2006; Gloag et al. 2013; De Mársico and Reboreda 2014; Fiorini et al. 2014), to avoid attacking their own previously laid eggs. For this reason, once a nest is parasitized, it would be adaptive to remove it from the subject's register of host nests potentially suitable for subsequent visits during a given hosts' nesting attempt ('book-keeping hypothesis'; Reboreda et al. 1996; Clayton et al. 1997). This dynamic form of spatial memory resembles the problems faced by caching animals, which must remember where they hide food and then update the information as they collect it. Both behaviour specializations may place increased demand on spatial memory. Consistently with the hypothesis that brood parasitism imposes spatial demands, it has been reported that female cowbirds possess a larger hippocampus (Sherry et al. 1993; Reboreda et al. 1996), greater accurate spatial memory (Guigueno et al. 2014) and higher levels of hippocampal neurogenesis (Guigueno et al. 2016) than conspecific males.

Information about nest visiting has hitherto been indirectly derived from observations of parasitism or egg destruction made exclusively at the nests, and as a consequence, very little is known about prospecting behaviour prior to laying. It is not known, for instance, how far in advance do females locate nests prior to parasitize them, whether they visit potential targets multiple times and whether they return assiduously after laying, either to repeat parasitic attacks or to monitor nest progress (but see Gloag et al. 2014).

We used a novel passive digital radio tracking method to monitor female nest visitation sequences in two species of cowbirds: the shiny cowbird, *M. bonariensis*, a generalist brood parasite that shows high laying synchronization with host laying (Mermoz and Reboreda 1999; Fiorini and Reboreda 2006; Astié and Reboreda 2009), and the screaming cowbird, *Molothrus rufoaxillaris*, a specialist parasite that shows poor synchronization with its almost exclusive host, the baywing, *Agelaioides badius* (Fraga 1998; De Mársico and Reboreda 2008). It has been proposed that the lack of synchronization between screaming cowbird parasitism and baywing laying may be the result of unpredictable behaviour of baywings, as they can delay the start of laying after nest completion from 1 to 19 days, possibly as an adaptation against parasitism (De Mársico and Reboreda 2008).

The technology used allowed us to monitor the visits in a 20–30-m-radius area around the nest. This is particularly important because brood parasites such as cuckoos and cowbirds can locate nests without need to get very close to them, as they can observe host activity during nest building (Wyllie 1981; Wiley 1988; Kattan 1997; Teuschl et al. 1998; Banks and Martin 2001; Robinson and Robinson 2001). Nest-centred studies (e.g. microcameras, Gloag et al. 2013) cannot assess cowbird activity around the nest and hence give an incomplete picture of prospecting behaviour biased towards underestimating the amount of prospecting.

Our goal was to establish the pattern of nest prospecting in shiny and screaming cowbirds, testing the expectation that parasitized nests are visited ahead of laying visits. The unpredictable start of laying in the host of the screaming cowbird means that, relative to the shiny cowbird attacking mockingbirds, a rather predictable host, screaming cowbirds, may have higher need for prospecting visits. This is because a single visit to a mockingbird nest is informative about its state, but the same is not true for baywings due to their long and variable time gap between nest construction and laying onset. Finally, while, as mentioned previously, there is some evidence showing that generalist parasites such as shiny and brown-headed cowbirds avoid revisiting nests in which they have laid an egg, it is unknown whether this also occurs in our specialist model (the specialist screaming cowbird) for which the reproductive scenario is markedly different.

Methods

Study site

We conducted the study at reserve ‘El Destino’ (35° 08′ S, 57° 23′ W), near the town of Magdalena, Buenos Aires Province, Argentina, during the breeding seasons (October–February) 2012–2013 and 2013–2014. The study area comprises approximately 500 ha of flooding grasslands with interspersed woodland patches dominated by *Celtis ehrenbergiana* and *Scutia buxifolia*. Shiny and screaming cowbirds are year-round residents in the area.

Data collection

We captured 37 shiny cowbird females (20 during 2012 and 17 during 2013) and 37 screaming cowbird females (17 during 2012 and 20 during 2013) using walk-in traps and mist nests and instrumented them with 1.0-g coded radio tags (model NTQB-4-2, Lotek Wireless, Ontario, Canada) using the Rappole harness technique (Rappole and Tipton 1991). Three shiny and two screaming cowbird females were instrumented during both breeding seasons. The radio tags were designed to run for 79 days emitting ID-coded radio pulses on a single frequency (150.360 MHz) every 2 s. For shiny cowbirds, the weight of the radio tag ranged between 1.7 and 2.3% of the female body mass, while for screaming cowbirds, it ranged between 1.7 and 2.1%. The radio tag had no obvious effects on cowbirds’ behaviour, since females visited nests and parasitized them as soon as 18 h after tag deployment (SM1).

We recorded shiny and screaming cowbird visits to mockingbird and baywing nests using a digitally encoded proximity data logger (DataSika, Biotrack, Wareham, UK) connected to an omnidirectional antenna (Biotrack, Wareham, UK) and to a 12-V car battery. The data loggers continually ‘listened’ for nearby tags and recorded the tag identity code, date, time and signal strength (arbitrary units between 0 and 255, inversely related to receiver-transmitter distance), whenever a tagged cowbird came within detection range (approximately 30 m from the antenna).

We placed the data loggers on the ground directly below 29 mockingbird, *Mimus saturninus*, and 16 baywing nests that were in the construction or prelaying stages (i.e. the time since nest lining is completed until the host lays its first egg). We continuously monitored nest activity, from the moment that the data logger was deployed until 3–4 days after the onset of incubation or nest failure (i.e. abandonment or depredation), whichever occurred first. We monitored 156 nest-days in mockingbirds (29 nests, range 2–11 days per nest) and 150 nest-days in baywings (16 nests, range 5–23 days per nest). Mounting and dismounting the data logger, antenna and battery were done as quickly as possible (less than 5 min) to minimize nest disturbance.

In mockingbird nests, we supplemented data logging with video recordings, using a camera (Handykam 420 CCD colour microcamera) suspended above the nest and connected to a digital video recorder (Lawmate PVR1000 or PVR500 ECO) placed at the base of the tree. Additionally, we tracked females using standard radio telemetry with a receiver for coded radio tags (SRX-400A, Lotek Wireless, Ontario, Canada) to check whether tagged cowbirds that were not seen near the nests remained in the study area. It was not possible to record data blind because our study involved focal animals and nests in the field.

Data analysis

We operationally defined a nest visit as a set of contiguous data logger records, selecting the time gap between records suitable to treat signals as independent visits through a sensitivity analysis. This analysis served to minimize two types of errors: (1) considering two visits as independent when the cowbird had remained nearby but there was an interval without records due to signal obstruction by vegetation and (2) considering as a single-visit cases where the female effectively left the host territory and came back between two temporally close records.

To choose the optimal criterion, we calculated the number of visits that resulted for increasing values of interval without signal (5, 10, 15 s, etc.). In this way, the longer the time interval, the fewer the visits. Next, we fitted an exponential function to this data and calculated the percentage of variation in the number of visits for fixed increasing values of interval without signal. The interval without signal selected to consider two visits as independent was the one where the percentage of remaining variation in the number of visits as a function of time was only 5%, resulting in 24.7 s for shiny cowbirds and 22.2 s for screaming cowbirds.

Then, we classified visits in two different types according to whether the cowbird was less or more than 10 m from the nest. Our distance estimates are subject to noise because recorded signal strength is affected (besides distance) by habitat structure, tag height above ground and relative orientation between receiver and tag antenna (Rutz et al. 2012). Hence, to assign each visit to a distance class, it was necessary to generate calibration data. To do this, we measured signal strength as a function of distance when placing receiver stations in both chalk-browed mockingbird (*n* = 5) and baywing (*n* = 5) nests chosen at random from the pool of monitored nests and displacing a radio tag attached to the top of a 4-m pole placed at 15 different distances from the receiver stations: 1, 3, 5, 7, 9, 11, 13, 15, 17, 19, 21, 25, 29, 35 and 40 m. At each position, we rested the pole on the ground so that the tags were consistently 4 m above the ground, in an orientation that matched that of an approaching cowbird. We repeated the procedure in the four cardinal directions from the nest to account for variation in vegetation.

We followed the methodology of Mennill et al. (2012) to estimate a signal strength threshold that would be consistent with a tag emitting pulses from closer or further than 10 m from the receiver. First, we grouped tag test data in 5-m bins and generated box plots with the data in each bin. Next, we calculated the threshold as the mid-point between the lower 25th percentile of the 6–10-m tag test data and the upper 25th percentile of the 11–15-m tag test data, resulting in signal strength of 114.3 (arbitrary units). Thus, records with signal strength stronger than this value were considered visits to a distance of less than 10 m from the nests, while records with signal strength weaker than this value were considered visits farther than 10 m from the nests. Additionally, we used the records obtained during parasitic events (visits in which egg laying by the cowbird was independently verified) to test the accuracy of the calibration. Signal strength detected during shiny cowbird parasitic events in mockingbird nests was 176 ± 8.0 (mean ± SE, *n* = 5), while that detected during screaming cowbird parasitic events in baywing nests was 127 ± 12.6 (mean ± SE, *n* = 11). These values were consistent with the threshold defined during calibration. The signal strength recorded when the radio tag was inside the nest was not the highest one recorded during calibration, probably because the structure of the nest (open cup in mockingbirds and closed in baywings) obstructs the signal when the receiver is placed on the ground below the nests.

We standardized the time of visits relative to sunrise on the day of recording (US Naval Observatory data, http://www.usno.navy.mil/). For each parasitic event, we analysed if there were records of previous visits of the parasitic female to that nest and its temporal sequence. We also analysed if the female returned to the nest after parasitism and if there were events of repeat parasitism.

For each female, we calculated the frequency of visits before and after parasitism as the number of visits to a nest in the period that the data logger was active. To compare the time of parasitic visits between species, we used records from the data loggers and data from video recordings. Values reported are means ± SE.

Results

Visits to host nests by shiny and screaming cowbird females

Table 1 indicates the main characteristics of visits to host nests by tagged shiny and screaming cowbird females.

Visits to mockingbird nests by shiny cowbird females occurred throughout the day (Fig. 1a). The frequency of parasitism by tagged and untagged shiny cowbird females in the monitored nests was 79% (22/28 nests; for one nest, we were unable to determine whether it was parasitized), with an intensity of 3.5 ± 0.4 parasitic eggs per parasitized nest (*n* = 22 nests, range = 1–7 eggs). Tagged females laid eggs in 5 of 22 (23%) parasitized nests, and in all cases, the tagged female laid one egg. We video recorded eight additional parasitic events by untagged females. Shiny cowbird parasitic events occurred from 29 min before sunrise to 26 min after sunrise and were preceded by at least one visit of the same female to less than 10 m from the nest (range = 1–8 visits; Table 2 and Fig. 2). The latency between the final visit and the parasitic event was determined for three cases and it was 1, 1 and 3 days (Table 2). One of the five females revisited twice the nest where she had already laid an egg, but there were no cases of repeat parasitism.

Visits by screaming cowbirds to baywing nests were also distributed throughout the day. Most visits occurred during the first 7 h after sunrise (65% of the visits,

Table 1 Main characteristics of visits by shiny and screaming cowbird females to monitored host nests

	Shiny cowbird	Screaming cowbird
Number of tagged females recorded	14	27
Number of recorded visits	223	631
Number of nests visited	22	14
Median and range of number of nests visited per tagged female	4 (1–10)	2 (1–5)
Median and range of number of females per nest	2 (0–5)	3.5 (0–10)
Median and range of max distance between nests (m)	625 (178–982)	710 (50–1323)
Median and range of length of visits (s)	24 (4–568)	34 (4–837)
Earliest non-laying visit	4 min after sunrise	At sunrise
Latest non-laying visit	13 h 33 min after sunrise	14 h 21 min after sunrise

For each species, we report the following: number of tagged females recorded, total number of visits recorded in monitored nests, total number of host nests visited by tagged females, median and range of number of different females visiting each monitored nest, median and range of number of different nests visited by a single female, median and range of number of different females visiting a single nest, maximum distance between nests visited by a single female, median and range of length of the visits and time of the earliest and latest non-laying visits

Fig. 1b). The frequency of parasitism by tagged and untagged screaming cowbird females in monitored baywing nests was 88% (14/16 nests), with an intensity of parasitism of 4.8 ± 0.8 parasitic eggs per parasitized nest (n = 14 nests, range = 1–10 eggs). Tagged females laid eggs in 7 of 14 (50%) parasitized nests (11 parasitic events by 7 tagged females, Table 3). Tagged females laid, on average, 1.6 ± 0.8 eggs per nest (range 1–2 eggs).

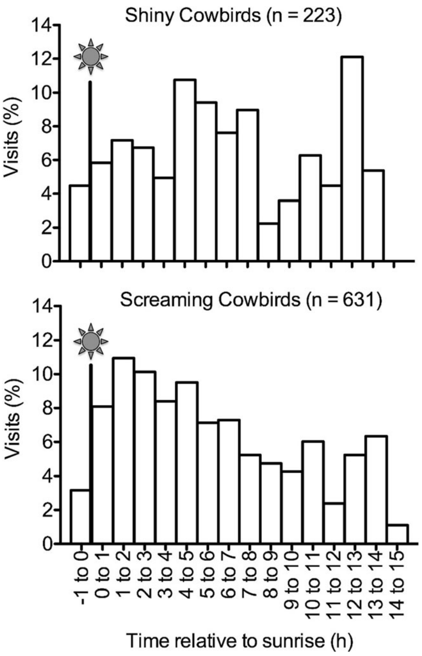


Fig. 1 Temporal distribution of visits by **a** shiny cowbird females to chalk-browed mockingbird (*Mimus saturninus*) nests (n = 223 total visits from 14 different females each making 1 to 15 visits to the same nest) and **b** screaming cowbird females to baywing (*Agelaioides badius*) nests (n = 631 total visits from 27 different females each making 1 to 90 visits to the same nest). The *bars* show the percentage of visits in 1-h intervals since 1 h before sunrise

Parasitic events by tagged screaming cowbird females occurred from 54 to 40 min before sunrise and were preceded by at least one visit of the same female to less than 10 m from the nest (Table 3 and Fig. 3). The latency between the final non-laying visit and the parasitic event varied between 1 and 4 days (Table 3). All the females repeatedly revisited the nest where they had already laid an egg (range 2–39 visits in the 0–9 days following the parasitic event). Repeat parasitism was recorded for two of the seven females (Fig. 3).

Comparison between species

The mean number of visits per nest was higher (Mann-Whitney U test: U = 100.5, p = 0.02, shiny cowbirds n = 14, screaming cowbirds n = 27), and parasitism visits occurred earlier (Mann-Whitney U test: U = 137, p < 0.001, shiny cowbirds n = 13, screaming cowbirds n = 11) in screaming than in shiny cowbirds. The proportion of females that revisited host nests after parasitism was higher in screaming than in shiny cowbirds (screaming cowbirds 7/7, shiny cowbirds 1/5, Fisher's exact test: p = 0.01).

Discussion

In avian brood parasites, evidence that females use activity during nest building to locate host nests comes from studies in the common cuckoo, *Cuculus canorus* (Wyllie 1981; Honza et al. 2002), the great spotted cuckoo, *Clamator glandarius* (Soler and Pérez-Contreras 2012), the brown-headed cowbird (Clotfelter 1998; Banks and Martin 2001; Robinson and Robinson 2001) and the shiny cowbird (Wiley 1988; Kattan 1997; Fiorini and

Table 2 Details of the events of parasitism conducted by radio-tagged shiny cowbird females in chalk-browed mockingbird (*Mimus saturninus*) nests

Nest	Female	Date	Time	Time relative to sunrise (min)	*N* previous visits (<10 m)	Days of visits (<10 m)	*N* previous visits (>10 m)	Days of visits (>10 m)
Ms 8–2	2642	30 November 12	5:55	26	–	–	–	–
Ms 15–4	2681	05 December 12	4:59	−29	2	−1	0	–
Ms 6–4	2874	13 December 12	5:00	−29	8	−8 to −1	6	−7 to −1
Ms 3–5	3850	24 December 12	5:08	−26	1	−3	3	−3 to −2
Ms 35	2681	29 November 13	5:18	−11	–	–	–	–

For each event, we report the following: the nest and female identifications; the date, absolute time and time relative to sunrise on the day of parasitism; the number of visits to less or more than 10 m from the nest the previous days to the event of parasitism; and the range of days at which the visits occurred. For the events of female 2642 in nest 8–2 and female 2681 in nest 35, we do not have information of number and date of previous visits because female 2642 was instrumented the day before the event of parasitism and receiver in nest 35 was mounted the day before the event of parasitism

Reboreda 2006). However, the majority of these studies (with the exception of Honza et al. 2002 and some records by Peer and Sealy 1999) did not analyse the prospecting behaviour of host nests by individual females. Thus, questions about the timing and frequency of prospective and post-parasitism visits remained open.

We used a novel passive digital radio tracking method to monitor nest visits by shiny and screaming cowbird females. The use of proximity data loggers allowed us to record all visits conducted by tagged females during prelaying, laying and early incubation; quantifying length of visits; and, using signal strength, proximity to the nest. Visiting nests before laying allows parasite females to acquire information that is necessary to target host nests appropriately at a time (before sunrise) when nest detection is hard. Shiny and screaming cowbird females may use two cues to target host nests for

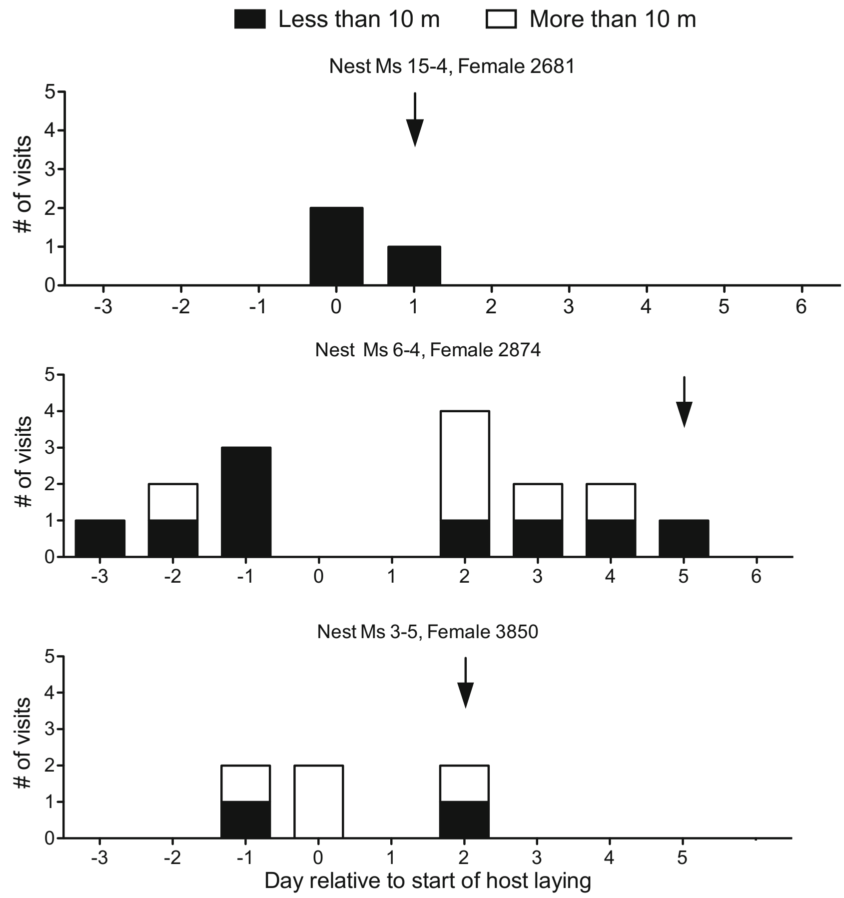


Fig. 2 Temporal sequence of visits to chalk-browed mockingbird (*Mimus saturninus*) nests by three radio-tagged shiny cowbird females. *Bars* indicate the number of visits to less and more than 10 m from the nest, and *numbers* on the *X*-axis indicate the days relative to the start of host laying (day 0). The *arrows* indicate the day of the parasitic event

Table 3 Details of the events of parasitism conducted by radio-tagged screaming cowbird females in baywing (*Agelaioides badius*) nests

Nest	Female	Date	Time	Time relative to sunrise (min)	*N* previous visits (<10 m)	Days of visits (<10 m)	*N* previous visits (>10 m)	Days of visits (>10 m)
Ab 16	2686[a]	19 December 12	4:39	−52	14	−3 to −1	22	−3 to −1
Ab 16	2686[a]	22 December 12	4:40	−53	14 + 7	−6 to −1	22 + 4	−6 to −1
Ab 16	2877	21 December 12	4:47	−45	4	−2 to −1	8	−3 to −1
Ab 24	2644	30 December 12	4:53	−45	1	−2	0	–
Ab 40 1–2	2686	26 January 12	5:09	−54	2 + 2[c]	−9 to −1	19 + 17[c]	−9 to −1
Ab 8	2451[b]	22 December 13	4:47	−45	8	−7 to −1	16	−7 to −1
Ab 8	2451[b]	25 December 13	4:44	−50	8 + 2	−10 to −1	16 + 5	−11 to −1
Ab 25	2441	25 December 13	4:53	−41	–	–	–	–
Ab 25	2457	27 December 13	4:55	−40	10	−3 to −1	17	−3 to −1
Ab 20	2186	12 January 14	5:02	−46	1	−4	8	−7 to −1
Ab 31	2441	14 January 14	5:06	−44	2	−3 to −2	1	−2

For each event, we report the following: the nest and female identifications; the date, absolute time and time relative to sunrise on the day of parasitism; the number of visits to less or more than 10 m from the nest the previous days to the event of parasitism; and the range of days at which the visits occurred. For the event of female 2441 in nest 25, we do not have information of number and date of previous visits because the receiver was mounted the day before the event of parasitism

[a] Corresponds to cases of repeated parasitism

[b] Corresponds to cases of repeated parasitism

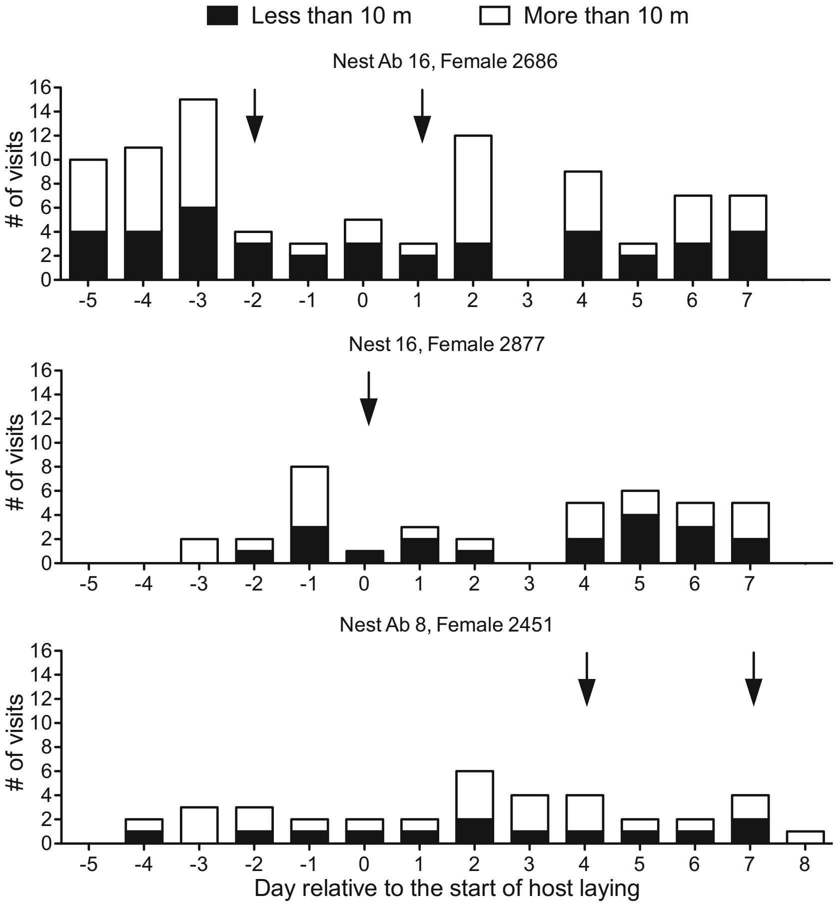
[c] Corresponds to visits to the first and second (N40-2) laying attempt of the host

parasitism: the stage of nest building (a nest with complete inner lining predicts the start of laying) and the start of host egg laying (namely the presence of eggs). In both cases, the parasite needs to visit repeatedly potential host nests. These cues may be redundant for shiny cowbirds, because mockingbirds and other common hosts start laying immediately after the inner lining of the nest is complete. For screaming cowbirds, however, nest building cues are not very informative, as baywings can delay the start of laying from 1 to 19 days after nest inner lining is complete (De Mársico and Reboreda 2008). This unpredictability may be the adaptive reason for screaming cowbirds to show a much greater number of prospecting visits than shiny cowbirds.

Gloag et al. (2014) reported that shiny cowbirds rarely returned to lay a second egg in the nest that they parasitized (i.e. repeat parasitism). Our results replicate and extend their finding, showing that shiny cowbird females rarely revisit not just nests themselves, but also the proximity of any nest that they have parasitized. This is consistent with the notion that once a nest is parasitized, the female somehow ‘labels’ it in her register of nests in her home range (‘bookkeeping hypothesis’; Reboreda et al. 1996; Clayton et al. 1997). By avoiding revisiting the nests that she parasitized, shiny cowbird females eliminate the cost of potential destruction of their own previously laid eggs, as they peck eggs when visiting host nests, and this behaviour may result in the puncture of both host and parasite eggs (Fiorini et al. 2014; Gloag et al. 2014). Notice that just erasing the nests from memory would not work, since it might lead to rediscovery and, hence, reparasitizing nests more than once. The capacity of shiny cowbird females of remembering nests and what may be called their parasitic affordances (namely whether the nest is approaching suitability, is likely to be suitable next morning or not suitable anymore because it has been used and/or the host has started incubation) may be akin to a form of ‘episodic-like memory’ (Clayton et al. 2001), as the parasite benefits by remembering precise features of a specific event, such as the location and status of each nest and her own act of laying in them.

Furthermore, by avoiding interaction with the host, cowbirds may avoid influencing the host’s decision to reject or abandon the clutch. In yellow warblers (*Dendroica petechia*), hosts of brown-headed cowbirds, the probability of burial of the parasitized clutch is higher if they interact with an adult parasite in addition to receiving an artificial cowbird egg at their nest (Guigueno and Sealy 2011). In the same way, great reed warblers (*Acrocephalus arundinaceus*) reject artificial cuckoo eggs more often when they are presented with a stuffed cuckoo accompanied by the recording of a female cuckoo call (Bártol et al. 2002). Thus, both the avoidances of revisiting a nest that has already been parasitized and of visiting the vicinity of the nest are two ways in which parasites may reduce the probability of interacting with the host.

Fig. 3 Temporal sequence of visits to baywing (*Agelaioides badius*) nests by three radio-tagged screaming cowbird females. *Bars* indicate the number of visits to less and more than 10 m from the nest, and *numbers* on the *X*-axis indicate the days relative to the start of host laying (day 0). The *arrows* indicate the day of the parasitic event. The *upper* and *lower graphics* show cases of repeated parasitism



The species differences that we recorded reflect functional considerations. Nest visits prior to parasitism were more frequent in screaming than in shiny cowbirds, and screaming cowbirds visited host nests repeatedly after laying and, in some cases, parasitized them more than once, rather than avoiding parasitized nests as shiny cowbirds do. The hypothetical adaptive explanations for these differences relate to the fact that screaming cowbirds parasitize almost exclusively the baywing (Fraga 1998), a host with an unpredictable onset of laying. In addition, once baywings start laying, if heavily parasitized, they eject the entire clutch and lay a replacement clutch in the same nest (Fraga 1998; De Mársico et al. 2013). Thus, it seems adaptive for screaming cowbird females to visit repeatedly baywing nests before parasitism, to synchronize parasitism with host laying and, after parasitism, to detect events of clutch ejection. The greater incidence of repeat parasitism in screaming than in shiny cowbirds may relate to the specialism of the former. By using only one host, the specialist screaming cowbird is better adapted to evolved antiparasitic defences of its host, such as mimicry and seasonal timing of laying (De Mársico and Reboreda 2008; De Mársico et al. 2012), but there is a cost to be paid: host nests have much lower density than for the generalist sister species. The cost of reparasitizing a given nest may be worth paying given the scarcity of hosts. An additional factor is that baywings have helpers at the nest (Ursino et al. 2011), while the common hosts of the shiny cowbirds, including the chalked-browed mockingbird, do not. As a consequence of the cooperative reproductive system, brood reduction in baywing nests is rarer (De Mársico and Reboreda 2014), probably because the cost of feeding extra parasite chicks is attenuated if larger broods recruit more helpers to share the nest provisioning effort (Ursino et al. 2011).

The present study provides further insights into information use and nest visitation behaviour by brood parasites, supporting the prospecting hypothesis for such species and offering an opportunity for field biology to examine comparative aspects of cognition and memory under natural circumstances. The differences between prospecting strategies between our specialist and generalist model species add interesting details regarding the adaptive connotations of host specialization, but the generality of these differences needs to be tested by comparisons between other phylogenetically related sets of species.

Acknowledgements We thank Fundación Elsa Shaw de Pearson for allowing us to conduct this research in Reserva El Destino and Victoria Weinsztok and Cynthia Ursino for help in the field. RCS was supported by a scholarship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). VDF and JCR are research fellows of CONICET. This work was supported by grants from Agencia Nacional de Promoción Científica y Tecnológica and the University of Buenos Aires. All work complied with Argentinean law.

Compliance with ethical standards

Funding The study was funded by research grants of the University of Buenos Aires (W808) and Agencia Nacional de Promoción Científica y Tecnológica (PICT-2011-0045).

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The study was conducted with the permission of the Provincial Organism for Sustainable Development (OPDS, Buenos Aires, Argentina) and complies with the current laws of Argentina.

Informed consent Not applicable.

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