

1 Planning host exploitation through prospecting visits by parasitic cowbirds

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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, *M. rufoaxillaris*, in the periods preceding and overlapping the laying period of their hosts. Our goal was to examine the hypothesis that during pre-laying visits cowbird females form a dynamic memory library of laying opportunities, which they deploy to target suitable nests at a later pre-dawn 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 re-visiting 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 "book-keeping". 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.

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 (*B. 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 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,

M. bonariensis: Gloag et al. 2014), females rarely return to lay eggs in nests 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 specialisations 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, *Molothrus 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, *M. 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 synchronisation 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 one 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 above, 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 nets 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 2 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 seconds. 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 pre-laying 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 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 was done as quickly as possible (less than 5 min) to minimize nest disturbance.

In mockingbird nests, we supplemented datalogging 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 s, 10 s, 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 m, 3 m, 5 m, 7 m, 9 m, 11 m, 13 m, 15 m, 17 m, 19 m, 21 m, 25 m, 29 m, 35 m and 40 m. At each position, we rested the pole on the ground so that 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 \pm SE, $n=5$) while that detected during screaming cowbird parasitic events in baywing nests was 127 ± 12.6 (mean \pm 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 (U.S. 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 the data-logger was active. To compare the time of parasitic visits between species, we used records from the dataloggers and data from video-recordings. Values reported are means \pm SE.

RESULTS

Visits to host nests by shiny and screaming cowbird females

Table 1 indicates 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 8 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 3 cases and it was 1, 1 and 3 days (Table 2). One of the five females re-visited 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, 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).

Parasitic events by tagged screaming cowbird females occurred from 54 min 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 2). All the females repeatedly re-visited 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 2 of the 7 females (Fig. 2).

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 re-visited 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 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 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 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 (‘book-keeping hypothesis’; Reboreda et al. 1996; Clayton et al. 1997). By avoiding revisiting the nests 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 re-parasitizing nests more than once. The capacity of

324 shiny cowbird females of remembering nests and what may be called their parasitic
325 affordances (namely whether the nest is approaching suitability, is likely to be suitable next
326 morning, or not suitable anymore because it has been used and/or the host has started
327 incubation) may be akin to a form of 'episodic like memory' (Clayton et al. 2001) as the
328 parasite benefits by remembering precise features of a specific event, such as the location and
329 status of each nest and her own act of laying in them.

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

340 The species differences that we recorded reflect functional considerations. Nest visits
341 prior to parasitism were more frequent in screaming than in shiny cowbirds, and screaming
342 cowbirds visited host nests repeatedly after laying and in some cases parasitized them more
343 than once, rather than avoiding parasitized nests as shiny cowbirds do. The hypothetical
344 adaptive explanation for these differences relate to the fact that screaming cowbirds parasitize
345 almost exclusively the baywing (Fraga 1998), a host with an unpredictable onset of laying. In
346 addition, once baywings start laying, if heavily parasitized, they eject the entire clutch and lay
347 a replacement clutch in the same nest (Fraga 1998; De Mársico et al. 2013). Thus, it seems
348 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 defenses 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: hosts nests have much lower density than for the generalist sister species. The cost of re-parasitizing 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 behavior 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 models species adds 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.

COMPLIANCE WITH ETHICAL STANDARDS

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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 current laws of Argentina.

Informed consent: Not applicable

REFERENCES

- Alderson GW, Gibbs HL, Sealy SG (1999) Determining the reproductive behaviour of individual brown-headed cowbirds using microsatellite DNA markers. *Anim Behav* 58:895–905
- Arlt D, Pärt T (2008) Post-breeding information gathering and breeding territory shifts in northern wheatears. *J Anim Ecol* 77:211–219
- Astíe AA, Reboreda JC (2009) Shiny Cowbird parasitism of a low quality host: Effect of host traits on a parasite's reproductive success. *J Field Ornithol* 80:224–233
- Banks AJ, Martin TE (2001) Host activity and the risk of nest parasitism by brown-headed cowbirds. *Behav Ecol* 12:31–40
- Bártol I, Karcza Z, Moskát C, Røskft E, Kisbenedek T (2002) Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *J Avian Biol* 33:420–425
- Clayton NS, Griffiths DP, Emery NJ, Dickinson A (2001) Elements of episodic-like memory in animals. *Philos T Roy Soc B* 356:1483–1491
- Clayton NS, Reboreda JC, Kacelnik A (1997) Seasonal changes of hippocampus volume in parasitic cowbirds. *Behav Process* 41:237–243
- Clotfelter ED (1998) What cues do brown-headed cowbirds use to locate red-winged

397 blackbird host nests? Anim Behav 55:1181–1189

398 Davies NB (2000) Cuckoos, Cowbirds and Other Cheats. T & AD Poyser Ltd, London

399 De Mársico MC, Gantchoff MG, Reboreda JC (2012) Host-parasite coevolution beyond the
400 nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. Proc R
401 Soc Lond B 279:3401–3408

402 De Mársico MC, Gloag R, Ursino CA, Reboreda JC (2013) A novel method of rejection of
403 brood parasitic eggs reduces parasitism intensity in a cowbird host. Biol Lett
404 9:20130076

405 De Mársico MC, Reboreda JC (2008) Egg-laying behavior in screaming cowbirds: why does
406 a specialist brood parasite waste so many eggs? Condor 110:143–153

407 De Mársico MC, Reboreda JC (2014) High frequency but low impact of brood parasitism by
408 the specialist Screaming Cowbird on its primary host, the Baywing. Emu 114:309–316

409 Doligez B, Danchin E, Clobert J, Gustafsson L (1999) The use of conspecific reproductive
410 success for breeding habitat selection in a non-colonial, hole-nesting species, the
411 collared flycatcher. J Anim Ecol 68:1193–1206

412 Ellison K, Sealy SG, Gibbs HL (2006) Genetic elucidation of host use by individual
413 sympatric bronzed cowbirds (*Molothrus aeneus*) and brown-headed cowbirds (*M. ater*).
414 Can J Zool 84:1269–1280

415 Fiorini VD, Gloag R, Kacelnik A, Reboreda JC (2014) Strategic egg destruction by brood-
416 parasitic cowbirds? Anim Behav 93:229–235

417 Fiorini VD, Reboreda JC (2006) Cues used by shiny cowbirds (*Molothrus bonariensis*) to
418 locate and parasitise chalk-browed mockingbird (*Mimus saturninus*) nests. Behav Ecol
419 Sociobiol 60:379–385

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

- 423 Fraga RM (1998) Interactions of the parasitic Screaming and Shiny Cowbirds (*Molothrus*
 424 *rufoaxillaris* and *M. bonariensis*) with a shared host, the Bay-winged Cowbird (*M.*
 425 *badius*). In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts. Studies in
 426 coevolution. Oxford University Press, New York, NY, pp 173–193
- 427 Gloag R, Fiorini VD, Reboreda JC, Kacelnik A (2013) The wages of violence: mobbing by
 428 mockingbirds as a frontline defence against brood-parasitic cowbirds. *Anim Behav*
 429 86:1023–1029
- 430 Gloag R, Fiorini VD, Reboreda JC, Kacelnik A (2014) Shiny cowbirds share foster mothers
 431 but not true mothers in multiply parasitized mockingbird nests. *Behav Ecol Sociobiol*
 432 68:681–689
- 433 Guigueno MF, MacDougall-Shackleton SA, Sherry DF (2016) Sex and seasonal differences
 434 in hippocampal volume and neurogenesis in brood-parasitic brown-headed cowbirds
 435 (*Molothrus ater*). *Dev Neurobiol* (published online, doi:10.1002/dneu.22421)
- 436 Guigueno MF, Sealy SG (2011) Aggression towards egg-removing cowbird elicits clutch
 437 abandonment in parasitized yellow warblers, *Dendroica petechia*. *Anim Behav* 81:211–
 438 218
- 439 Guigueno MF, Snow DA, MacDougall-Shackleton SA, Sherry DF (2014) Female cowbirds
 440 have more accurate spatial memory than males. *Biol Lett* 10:20140026
- 441 Hahn DC, Sedgwick JA, Painter IS, Casna NJ (1999) A spatial and genetic analysis of
 442 cowbird host selection. *Stud Avian Biol-Ser* 18:204–217
- 443 Honza M, Taborsky B, Taborsky M, Teuschl Y, Vogl W, Moksnes A, Røskft E (2002)
 444 Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests
 445 before and during egg laying: a radiotelemetry study. *Anim Behav* 64:861–868
- 446 Kattan GH (1997) Shiny cowbirds follow the “shotgun” strategy of brood parasitism. *Anim*

447 Behav 53:647–654

448 McLaren CM, Woolfenden BE, Gibbs HL, Sealy SG (2003) Genetic and temporal patterns of
 449 multiple parasitism by brown-headed cowbirds (*Molothrus ater*) on song sparrows
 450 (*Melospiza melodia*). Can J Zool 81:281–286

451 Mennill DJ, Doucet SM, Ward K-AA, Maynard DF, Otis B, Burt JM (2012) A novel digital
 452 telemetry system for tracking wild animals: a field test for studying mate choice in a
 453 lekking tropical bird. Methods Ecol Evol 3:663–672

454 Mermoz ME, Reboreda JC (1999) Egg-laying behaviour by shiny cowbirds parasitizing
 455 brown-and-yellow marshbirds. Anim Behav 58:873–882

456 Moskát C, Barta Z, Hauber ME, Honza M (2006) High synchrony of egg laying in common
 457 cuckoos (*Cuculus canorus*) and their great reed warbler (*Acrocephalus arundinaceus*)
 458 hosts. Ethol Ecol Evol 18:159–167

459 Peer BD (2006) Egg destruction and egg removal by avian brood parasites: adaptiveness and
 460 consequences. Auk 123:16–22

461 Peer BD, Sealy SG (1999) Laying time of the Bronzed Cowbird. Wilson Bull 111:137–139

462 Pöysä H (2006) Public information and conspecific nest parasitism in goldeneyes: Targeting
 463 safe nests by parasites. Behav Ecol 17:459–465

464 Rappole JH, Tipton AR (1991) New harness design for attachment of radio transmitters to
 465 small passerines. J Field Ornithol 62:335–337

466 Reboreda JC, Clayton NS, Kacelnik A (1996) Species and sex differences in hippocampus
 467 size in parasitic and non-parasitic cowbirds. Neuroreport 7:505–508

468 Rivers JW, Peer BD (2016) Relatedness constrains virulence in an obligate avian brood
 469 parasite. Ornithol Sci 15:191–201

470 Rivers JW, Young S, Gonzalez EG, Horton B, Lock J, Fleischer RC (2012) High levels of
 471 relatedness between brown-headed cowbird (*Molothrus ater*) nestmates in a heavily

472 parasitized host community. Auk 129:623–631

473 Robertson RJ, Norman RF (1976) Behavioral defenses to brood parasitism by potential hosts
474 of the Brown-headed Cowbird. Condor 78:166–173

475 Robertson RJ, Norman RF (1977) The function and evolution of aggressive host behavior
476 towards the Brown-headed Cowbird (*Molothrus ater*). Can J Zool 55:508–518

477 Robinson SK, Robinson WD (2001) Avian nesting success in a selectively harvested North
478 temperate deciduous forest. Conserv Biol 15:1763–1771

479 Rothstein SI, Robinson SK (1998) Parasitic Birds and Their Hosts: Studies in Coevolution.
480 Oxford University Press, New York

481 Rutz C, Burns ZT, James R, Ismar SMH, Burt J, Otis B, Bowen J, St Clair JJH (2012)
482 Automated mapping of social networks in wild birds. Curr Biol 22:R669–671

483 Scardamaglia RC, Reboreda JC (2014) Ranging behavior of female and male shiny cowbirds
484 and screaming cowbirds while searching for host nests. Auk 131:610–618

485 Scott DM (1991) The time of day of egg laying by the brown-headed cowbird and other
486 icterines. Can J Zool 69:2093–2099

487 Seeley TD, Buhrman SC (2001) Nest-site selection in honey bees: How well do swarms
488 implement the “best-of-N” decision rule? Behav Ecol Sociobiol 49:416–427

489 Selonen V, Hanski IK (2010) Decision making in dispersing Siberian flying squirrels. Behav
490 Ecol 21:219–225

491 Sherry DF, Forbes MRL, Khurgel M, Ivy GO (1993) Females have a larger hippocampus
492 than males in the brood-parasitic brown-headed cowbird. P Natl Acad Sci USA
493 90:7839–7843

494 Smith JNM, Arcese P, McLean IG (1984) Age, experience, and enemy recognition by wild
495 song sparrows. Behav Ecol Sociobiol 14:101–106

496 Soler M, Pérez-Contreras T (2012) Location of suitable nests by great spotted cuckoos: an

497 empirical and experimental study. *Behav Ecol Sociobiol* 66:1305–1310
 498 Soler M, Pérez-Contreras T, Soler JJ (2015) Synchronization of laying by great spotted
 499 cuckoos and recognition ability of magpies. *J Avian Biol* 46:608–615
 500 Spottiswoode CN, Kilner RM, Davies NB (2012) Brood parasitism. In: Royle NJ, Smiseth
 501 PT, Kölliker M (eds) *The evolution of parental care*. Oxford University Press, Oxford,
 502 pp 226–243
 503 Teuschl Y, Taborsky B, Taborsky M (1998) How do cuckoos find their hosts? The role of
 504 habitat imprinting. *Anim Behav* 56:1425–1433
 505 Ursino CA, De Mársico MC, Sued M, Farall A, Reboreda JC (2011) Brood parasitism
 506 disproportionately increases nest provisioning and helper recruitment in a cooperatively
 507 breeding bird. *Behav Ecol Sociobiol* 65:2279–2286
 508 Van Nouhuys S, Ehrnsten J (2004) Wasp behavior leads to uniform parasitism of a host
 509 available only a few hours per year. *Behav Ecol* 15:661–665
 510 Wiley JW (1988) Host selection by the Shiny Cowbird. *Condor* 90:289–303
 511 Wyllie I (1981) *The Cuckoo*. Batsford, London
 512

SUPPLEMENTARY MATERIAL CAPTION

SM1. Video-recording of a tagged female shiny cowbird that makes a laying visit to a chalk-browed mockingbird nest, where she is mobbed by both mockingbirds while she lays her egg.

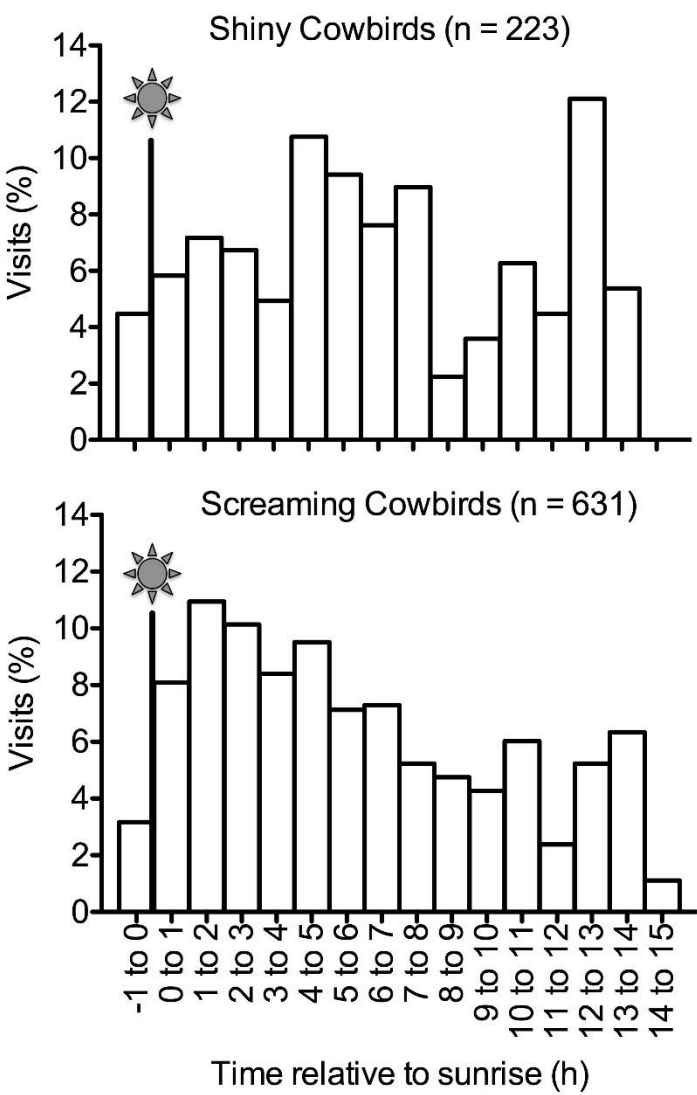
FIGURE LEGENDS

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 one-hour intervals since one hour before sunrise.

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 arrow indicates the day of the parasitic event

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 arrow indicates the day of the parasitic event. The upper and lower graphics show cases of repeated parasitism

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Figure 1

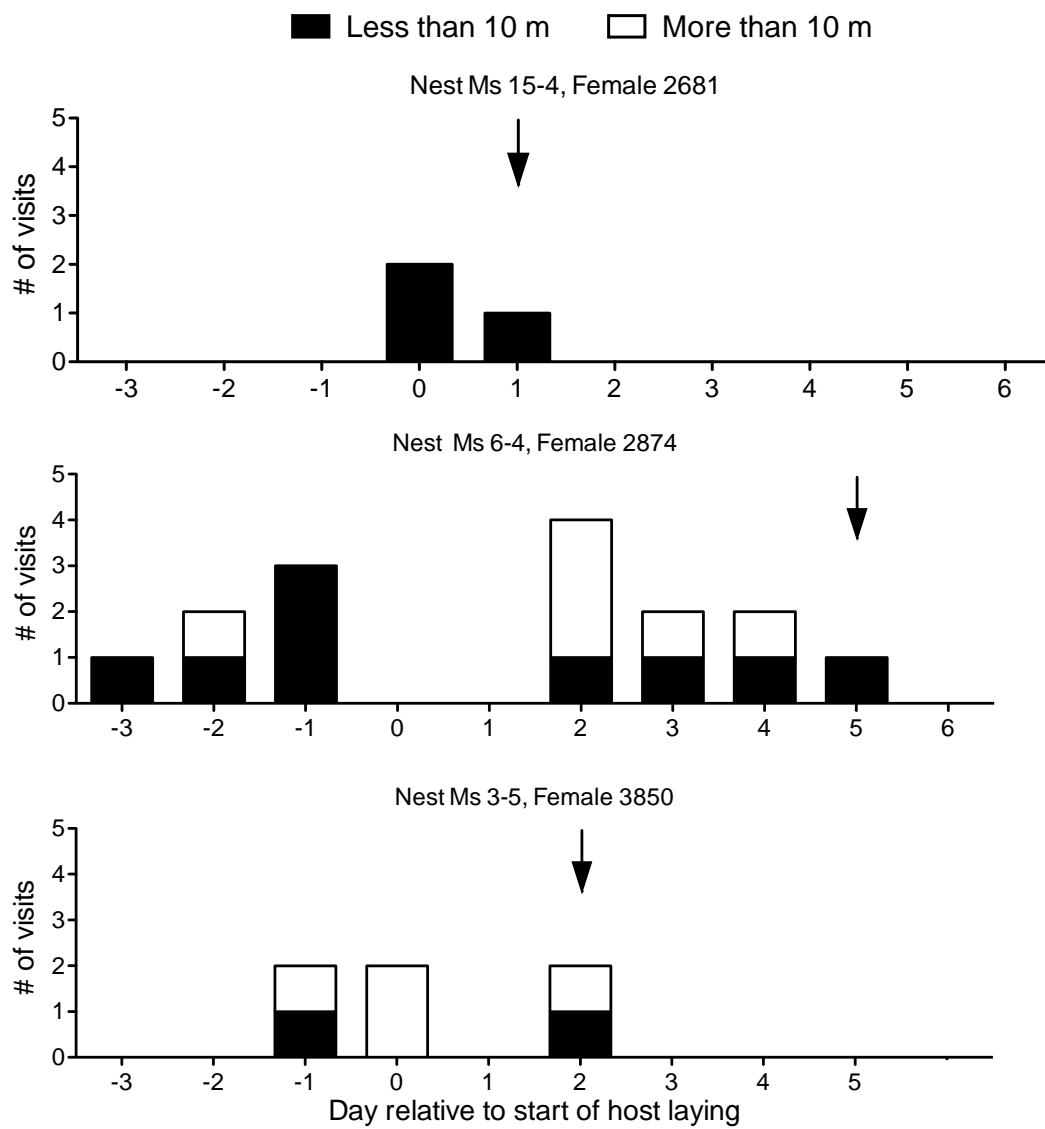


Figure 2

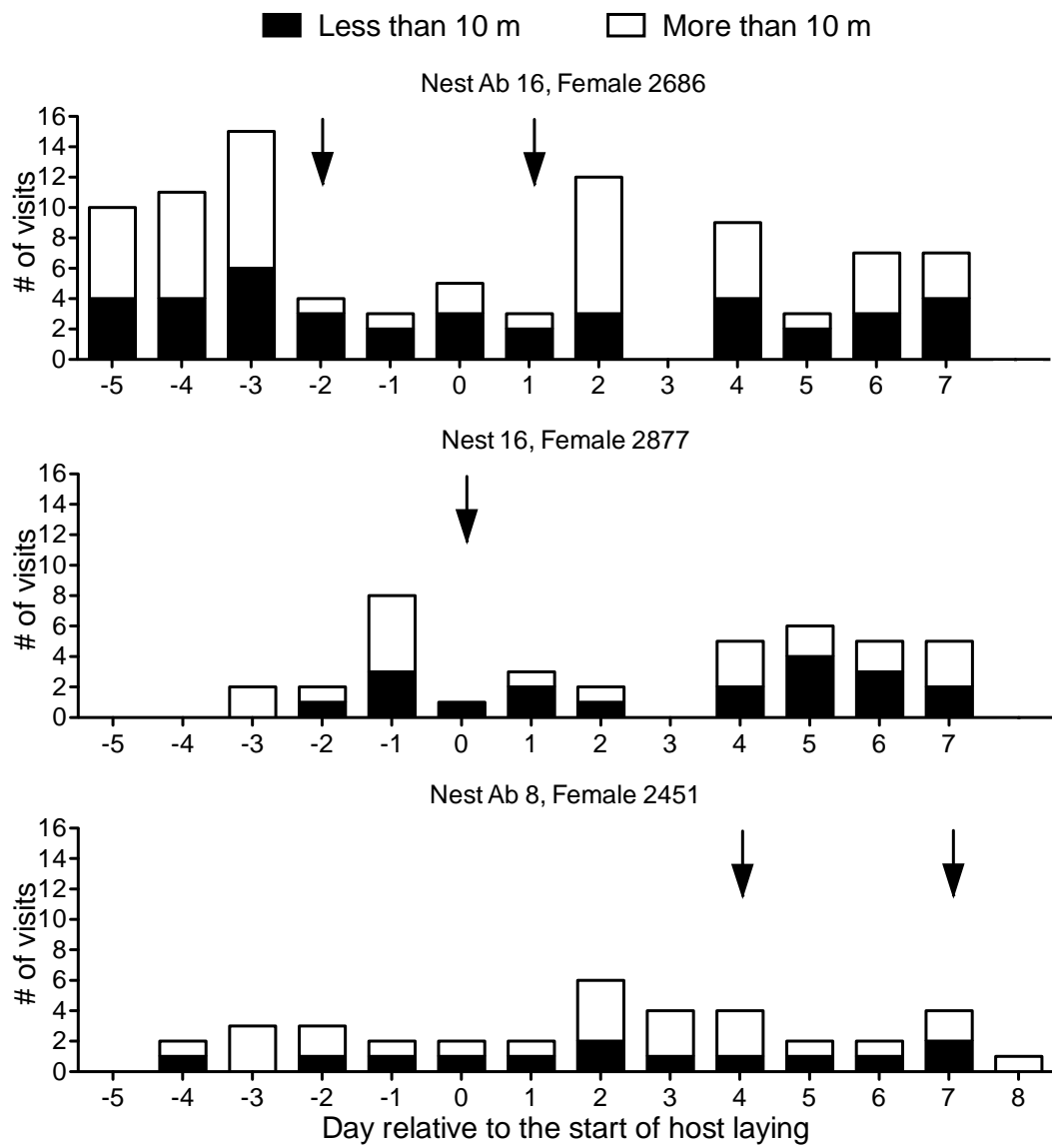


Figure 3

Table 1 Main characteristics of visits by shiny and screaming cowbird females to monitored host nests. For each species we report: 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

	<i>Shiny cowbird</i>	<i>Screaming cowbird</i>
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

Table 2 Details of the events of parasitism conducted by radio-tagged shiny cowbird females in mockingbird nests. For each event we report: 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

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

Table 3 Details of the events of parasitism conducted by radio-tagged screaming cowbird females in baywing (*Agelaioides badius*) nests. For each event we report: 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

<i>Nest</i>	<i>Female</i>	<i>Date</i>	<i>Time</i>	<i>Time relative to sunrise (min)</i>	<i>N previous visits (< 10 m)</i>	<i>Days of visits (< 10 m)</i>	<i>N previous visits (> 10 m)</i>	<i>Days of visits (> 10 m)</i>
Ab 16	2686 ¹	19/12/12	4:39	-52	14	-3 a -1	22	-3 a -1
Ab 16	2686 ¹	22/12/12	4:40	-53	14 + 7	-6 a -1	22 + 4	-6 a -1
Ab 16	2877	21/12/12	4:47	-45	4	-2 a -1	8	-3 a -1
Ab 24	2644	30/12/12	4:53	-45	1	-2	0	-
Ab 40 1-2	2686	26/01/12	5:09	-54	2 + 2 ³	-9 a -1	19 + 17 ³	-9 a -1
Ab 8	2451 ²	22/12/13	4:47	-45	8	-7 a -1	16	-7 a -1
Ab 8	2451 ²	25/12/13	4:44	-50	8 + 2	-10 a -1	16 + 5	-11 a -1
Ab 25	2441	25/12/13	4:53	-41	-	-	-	-
Ab 25	2457	27/12/13	4:55	-40	10	-3 a -1	17	-3 a -1
Ab 20	2186	12/01/14	5:02	-46	1	-4	8	-7 a -1
Ab 31	2441	14/01/14	5:06	-44	2	-3 a -2	1	-2

¹ and ² correspond to cases of repeated parasitism and ³ correspond to visits to the first and second (N40-2) laying attempt of the host