# Roosting behaviour is related to reproductive strategy in brood parasitic cowbirds

ROMINA C. SCARDAMAGLIA,[1]* (iD) ALEX KACELNIK[2] & JUAN C. REBOREDA[1] (iD)

[1]*Departamento de Ecología, Genética y Evolución & IEGEBA-CONICET, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina*

[2]*Department of Zoology, University of Oxford, Oxford OX1 3PS, UK*

Shiny Cowbirds *Molothrus bonariensis* and Screaming Cowbirds *Molothrus rufoaxillaris* are closely related brood parasites but the former is socially polygynous or promiscuous and an extreme host generalist, whereas the latter is socially monogamous and parasitizes almost exclusively one host. Females of both species lay in relative darkness, before dawn, relying for host nest location on previous days' prospecting activity, or possibly on following better-informed roost associates. We studied the temporal and spatial patterns of roosting behaviour in these species to test the hypothesis that roosting behaviour of cowbirds is related to their breeding strategy (brood parasitism) and reflects differences in strategies between species. We recorded fidelity to a roost, location fidelity within a roost, inter-individual spatial associations and timing of roost departures and parasitic events, using tagged individuals. Female Shiny Cowbirds and both sexes of Screaming Cowbirds showed marked fidelity in roosting location, and roost departures occurred both during and after the known time window for parasitism, with earlier departures probably corresponding to laying days. Screaming Cowbird females and males that were trapped together and showed high levels of association during the day, also showed high levels of association in the roost. We describe the spatial and temporal patterns of a relatively poorly known aspect of avian ecology in general and the behaviour of brood parasites in particular.

**Keywords:** bird assemblage, *Molothrus*, radio-tracking, site fidelity, space use.

It is common in many bird species for individuals to gather in groups ranging from a few to many thousands to spend the overnight resting period together (Dhondt *et al.* 2006, Winkler 2006, Laughlin *et al.* 2014). Although a widespread behaviour, the functional significance of communal roosting remains poorly understood and may have different explanations across taxa. Functions proposed for roosts include thermoregulation, reduction in probability of predation and information exchange; some studies have provided direct or indirect evidence for each of these factors in specific systems (Yom-Tov 1979, du Plessis *et al.* 1994, Paquet *et al.* 2016). An influential hypothesis elaborated by Ward and Zahavi (1973) proposed that bird assemblages such as roosts could act as information centres where individuals that do not have information on the location of good feeding sites can obtain such knowledge from individuals that do, but the empirical evidence is inconclusive and it is unlikely to apply equally across communally roosting species (Weatherhead 1987).

Only a few studies have analysed the activity of birds in roosts and, among those, most have focused mainly on two aspects: roost site fidelity (Morrison & Caccamise 1985, Conklin *et al.* 2007, Béchet *et al.* 2010, Laughlin *et al.* 2014) and roost-use in relation to feeding sites (Morrison & Caccamise 1985, 1990, Conklin *et al.* 2007, Adams 2011). These studies have shown great variability in roost site fidelity both between and within species. In Common Starlings *Sturnus vulgaris*, for example, some individuals remain highly

*Corresponding author.
Email: rscardamaglia@ege.fcen.uba.ar
Twitter: @rscardamaglia

faithful to a roost, whereas others frequently switch between different roosts in the area (Morrison & Caccamise 1985). Tree Swallows *Tachycineta bicolor* are faithful to a roost about 60% of the time. When swallows do switch roosts, they settle on those closer to their original roosting site rather than choosing randomly among the roosts in the area (Laughlin *et al.* 2014). However, Dunlin *Calidris alpina* use roosts that are closer to their last foraging locations than roosts that are also known to them and in which they have roosted before (Adams 2011). In addition, and contradicting expectations from the 'information centre' hypothesis for roost function (Ward & Zahavi 1973), Common Starlings were found to be more faithful to their diurnal feeding ranges than to their communal roosting sites, with birds commuting from up to five different communal roosts to a stable diurnal range (Morrison & Caccamise 1985).

Brood parasites, such as cuckoos and cowbirds, exploit the parental care of other species (hosts) by laying their eggs in the hosts' nests. The use of roosts in relation to brood parasites' reproductive strategy has not yet been studied, except for a few secondary or anecdotal mentions in studies analysing home-ranges and activity patterns in the Brown-headed Cowbird *Molothrus ater* (Thompson 1994, Gates & Evans 1998, Hahn *et al.* 1999) and one study that addressed roost departure times in Shiny Cowbirds *Molothrus bonariensis* (Feare & Zaccagnini 1993).

Females of the host generalist Shiny Cowbird and the host specialist Screaming Cowbird *Molothrus rufoaxillaris* lay their eggs around dawn (Gloag *et al.* 2013, Scardamaglia *et al.* 2017) in nests that they visited on previous days (Scardamaglia *et al.* 2017). It is known that cowbirds roost communally (Cruz *et al.* 1990, Feare & Zaccagnini 1993) and evidence suggests that they fly directly from their roost to target nests (Scardamaglia & Reboreda 2014). In addition to differences in the degree of specialization in host use, Shiny and Screaming Cowbirds differ in their mating systems: Shiny Cowbirds are socially polygynous or promiscuous and females search for nests without the assistance of the male, whereas Screaming Cowbirds are socially monogamous and the males accompany females when they search for nests (Mason 1987, Scardamaglia & Reboreda 2014). Social behaviour varies throughout the day: during the morning, individuals are found alone or in small groups, whereas

in the afternoon they gather to feed in larger flocks (Scardamaglia & Reboreda 2014, Kattan *et al.* 2016), grouping in communal roosts towards sunset. A similar behaviour has been observed in the Brown-headed Cowbird, a closely related species, in which males and females spend the morning in small groups in areas rich in host nests, joining large feeding flocks in the afternoon and roosting communally at night (Thompson 1994, Gates & Evans 1998).

In this study we test the hypothesis that roosting behaviour in cowbirds is related to their breeding strategy (brood parasitism) and reflects differences in strategies between species. The differences between the mating systems of Shiny and Screaming Cowbirds led us to expect differences in roosting behaviour between the males of the two species, but not between the females. We studied roosting site use at two different scales: we first studied fidelity between roosts (i.e. whether individuals joined one or more roost communities) and secondly, their location fidelity within a roost (i.e. whether individuals settled randomly within their roost each night or showed preference for particular locations). Because female Shiny Cowbirds search for nests in daytime and must reach the same nests in the following morning twilight, they face the navigational problem of reaching a different nest location every laying day in the dark. One might expect this to affect their choice of roosting site, but how is not obvious. As roosting may be constrained to dark, dense forest sites for predation reasons, Shiny Cowbirds may benefit from roosting at consistent locations in order to start laying expeditions in well-known areas. Host nests are typically in relatively open sites, where twilight navigation may be easier. On the other hand, if navigation towards host nests were not a problem, they could reduce the distance travelled for each laying trip by changing roosting site between nights. The same reasoning can be applied to both sexes of Screaming Cowbirds, which jointly visit host nests, but not to male Shiny Cowbirds, which do not participate in nest scouting or dawn-laying trips. Given their spatial association during the day and joint nest-searching, we expected Screaming Cowbird pairs to roost in close proximity. Furthermore, because laying occurs mostly during the dawn twilight, when low light intensity is unsuited to searching for nests or foraging, early roost departures may only occur on the fraction of days on which females are ready to lay.

## METHODS

### Study site and species

The study was conducted at the reserve 'El Destino' (35.141°S, 57.393°W), near the town of Magdalena, in Buenos Aires Province, Argentina, during the breeding seasons (October–February) 2010/2011 to 2013/2014. The area comprises ~500 ha of flooding grasslands with interspersed woodland patches dominated by two species of low, spiny trees, spiny hackberry *Celtis ehrenbergiana* and coronillo *Scutia buxifolia*. Screaming and Shiny Cowbirds are year-round residents in the area. At this field site Shiny Cowbirds intensely parasitize the Chalk-browed Mockingbird *Mimus saturninus* (frequency of parasitism 70–80%; Fiorini & Reboreda 2006, Gloag *et al.* 2012) and to a lesser degree other species such as the House Wren *Troglodytes aedon* (frequency of parasitism 50%; Tuero *et al.* 2007). Chalk-browed Mockingbirds breed from mid-September until mid-January and build open-cup nests in shrubs or trees with dense foliage, at a height of 1.5–2.5 m. They lay three to five eggs per clutch and, if a nest fails, the same pair may attempt re-nesting several times (Fraga 1985). Screaming Cowbirds parasitize exclusively the Greyish Baywing *Agelaioides badius*. The frequency of parasitism is 80–90% and most nests are parasitized multiple times (Mason 1980, Fraga 1998, De Mársico *et al.* 2010). Greyish Baywings rarely build their own nests. Instead, they breed in domed nests built by other species, secondary cavities or nestboxes (Friedmann 1929, Hoy & Ottow 1964, Fraga 1998, De Mársico *et al.* 2010). They breed from early December to late February and are cooperative breeders. Assisted pairs generally have one to three helpers, which are recruited after egg hatching (Fraga 1991, Ursino *et al.* 2011).

### Radiotelemetry

We trapped 36 Shiny Cowbirds (27 females and nine males) and 32 Screaming Cowbirds (27 females and five males) during the breeding seasons (October–February) 2010/2011 to 2013/2014 using either walk-in funnel traps baited with millet or mist-nets. The difference between the sexes in the number of birds trapped and tagged was due to the fact that in a concurrent project (Scardamaglia *et al.* 2017) we were more interested in female behaviour, resulting in a greater number of tagged females. Each bird was marked with a unique combination of colour plastic leg bands and a numbered aluminium band and was fitted with a radiotag. Two Shiny Cowbird females were tagged twice, in 2010/2011 and 2013/2014, and one female in three breeding seasons, in 2010/2011, 2011/2012 and 2013/2014. We used two different types of radiotags because this study was carried out simultaneously with two other projects (Scardamaglia & Reboreda 2014, Scardamaglia *et al.* 2017). During the breeding seasons 2010/2011 and 2011/2012 the animals were fitted with 1.2-g glue-on beeper-VHF radiotransmitters (model PicoPip Ag392 from Biotrack, Wareham, UK, or model A2455 from Advanced Telemetry Systems, Isanti, MN, USA). We glued the radiotransmitters to the back of the birds using cyanoacrylate adhesive and an activator (Loctite 401 and Loctite 770, Henkel, respectively). During the 2012/2013 and 2013/2014 breeding seasons the animals were fitted with 1.0-g backpack coded radiotags (model NTQB-4-2, Lotek Wireless, Newmarket, ON, Canada) using Teflon Ribbon (Bally Ribbon Mills, Philadelphia, PA, USA) and the Rappole harness technique (Rappole & Tipton 1991). The procedure of marking the cowbird and fitting the radio-transmitter lasted less than 15 min. These two different techniques yielded differences in the time the birds carried the transmitters. Birds fitted with glue-on radiotags carried them for $35.8 \pm 21.0$ days (mean $\pm$ sd, range = 6–68 days, $n = 34$, see Scardamaglia & Reboreda 2014), whereas those fitted with backpack tags carried them for the whole duration of tag life (tags were designed to run for 79 days). We found that the variables we measured (see below) did not differ significantly between tagging methods (see Supporting Information for more details). The radiotags had no obvious effects on cowbird behaviour, as females visited and parasitized nests as soon as 18 h after tag deployment (see SM1 in Scardamaglia *et al.* 2017).

To determine roost locations, we tracked cowbirds on foot, using the homing technique (White & Garrott 1990). Cowbirds were monitored around dusk using hand-held radiotracking receivers (beeper tags: model Sika, Biotrack; coded tags: model SRX-400A, Lotek Wireless). The coded tags hand-held receiver range was limited:

it required the distance between receiver and tag to be no more than ~50 m for proper code reading. Because some of the Screaming Cowbirds roosted in a deep forest area where access was difficult in the dark and impeded reliable identification of the birds, we present fewer data for this species. We recorded departure times from roosts using a hand-held receiver each morning from 04:30 to 06:30 h in 47, 34 and 29 days in the breeding seasons 2010/2011, 2011/2012 and 2013/2014, respectively. A departure was detected when the tag signal was recorded moving away (and eventually lost) from the fixed location the bird had maintained in the roost the previous night. During the day, we tracked cowbirds on foot to check that the radiotags were still active and that the birds remained in the area (and that any absence from the roost was not due to a faulty or lost radiotag).

To detect parasitic events from tagged females, in all seasons we video-recorded activity in mockingbird nests using a camera (Handykam 420 CCD colour micro-camera) suspended above the nest and connected to a digital video recorder (Lawmate PVR1000 or PVR500 ECO) placed at the base of the tree. We did not video record baywing nests, as they are prone to desert the nest if disturbed during the pre-laying or laying period (M.C. De Mársico pers. comm.). Additionally, during the seasons 2012/2013 and 2013/2014, we recorded tagged Shiny and Screaming Cowbird females visits to host nests using digitally encoded proximity data-loggers (DataSika, Biotrack) that were connected to an omnidirectional antenna (Biotrack) and to a 12-V car battery. The data-loggers continually 'listened' for nearby tags and recorded the tag identity code, date and time whenever a tagged cowbird came within detection range, ~30 m from the antenna (see Scardamaglia et al. 2017 for more details on recording of visits of tagged birds to host nests). We placed the data-loggers on the ground directly below 29 mockingbird and 16 baywing nests (Fig. 1) that were in the construction or pre-laying stages (defined as the time lapsed since nest lining is completed and the host lays its first egg). We monitored nest activity continuously 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. Overall, we monitored 156 nest-days of mockingbirds and 150 nest-days of baywings.

## Data analysis

We defined a roost operationally as an area where a group of birds gather to spend the night. Because there were clear breaks in the distribution of birds (see Results), we used these breaks to delimit discrete roosts. We used home-range data previously published for the cowbirds tracked during the first two breeding seasons (Scardamaglia & Reboreda 2014) to determine the distance between the individuals' resting locations and their diurnal locations (i.e. where they search for and locate host nests). To do this, we used the gCentroid function in rgeos package (Bivand & Rundel 2016) in R 3.3.1 (R Core Team 2017) to calculate both the diurnal range centroids and roost centroids and estimated the distance between these points for each individual.

### Fidelity to a roost
We defined fidelity to a roost as a percenatge: (no. of nights bird detected in roost/no, of nights bird was searched for) × 100. For this estimate we used data from birds that were monitored on at least four nights (maximum available 23 nights).

### Fidelity within a roost
To determine whether birds were faithful to the locations they used within a discrete roost, we compared the observed mean distance between night locations of each individual with the mean distance between locations of a simulated distribution of birds that settled within the roost at random each night. The simulation consisted of a Monte Carlo randomization procedure ($n = 1000$ runs) where bird locations along a linear roost could take integer values ranging from 0 m (the bird located in the same place in two different nights) to a maximum determined by the distance between opposite ends of the roost, with a 1-m resolution (see Supporting Information for more details of this simulation). We considered the observed distance to be significantly shorter than expected by chance if it fell below the 95th percentile of the distribution generated by the simulation.

### Association between Screaming Cowbird pairs
To investigate whether pairs of Screaming Cowbirds maintain their diurnal association during the night, we used data from three females and three males that had been captured in pairs (i.e.

**Figure 1.** Study area with area used during the day (polygon), roosting location centroids and locations of data-loggers (i.e. monitored host nests) with marked parasitism events for (a) Shiny Cowbirds and (b) Screaming Cowbirds.

individuals caught together in the same trap and showing high levels of association during the day; Scardamaglia & Reboreda 2014). As a control, we recorded the frequency of association in the roost of two males and two females that were caught separately (i.e. in the same trap but at different

times) and that did not show association during the day.

*Timing of roost departures and parasitism events*

We analysed the timing both of the departure of females from the roost and parasitism events by generating a frequency distribution of the timing of both sets of events at 5-min intervals and compared these between the two species using Mann–Whitney $U$-tests. The times of departures and parasitic events were standardized relative to sunrise on the day of recording for proper comparison, to account for variation in sunrise times through the season (http://www.usno.navy.mil/). The data presented here are not direct observations of females departing from the roost and arriving at a host nest to parasitize on the same day, because it was not logistically possible to record departure times for all tagged females each morning or to record activity at all potential target nests.

## RESULTS

### Characteristics of roosting locations

We recorded a total of 240 locations corresponding to 25 tagged Shiny Cowbird females (the other two tagged females were not detected in the area after tagging), 10 locations corresponding to five tagged Shiny Cowbird males (the other four tagged males were detected in the area during the morning but never around dusk, so they must have roosted outside our study area), 97 locations corresponding to 18 tagged Screaming Cowbird females (we did not record any roosting location for the other nine tagged females due to difficulty in accessing deep-forest locations) and 33 locations corresponding to the five tagged Screaming Cowbird males.

Radiotracked Shiny Cowbird females and both sexes of Screaming Cowbird mainly used one roost, which was maintained throughout the breeding season (see below). Tagged Shiny Cowbird males were rarely found in roosts in the study area. We detected a 'main roost' for Shiny Cowbirds, where a few hundred birds roosted each night and where 93% of locations of tagged birds were recorded. The distance between the opposite ends of this roost was 755 m and it was located along a band of trees next to a low-use road, adjacent to the diurnal home-ranges of the tagged birds (Fig. 1a). Other smaller roosts (of

only a few individuals) were recorded up to 4029 m apart. Screaming Cowbird roost locations were distributed in a band of forest (Fig. 1b). The distance between opposite ends in the distribution of birds was 1311 m.

The median distance between the roost centroid and the diurnal range centroid was 494.9 m (range = 219–889 m, $n = 13$) for Shiny Cowbird females, 966.7 m (range = 628–1646 m, $n = 8$) for Screaming Cowbird females and 974.5 m (range = 554–1710 m, $n = 5$) for Screaming Cowbird males.

### Fidelity to a roost

Female Shiny Cowbirds were faithful to one roost throughout the breeding season. On average, females returned to the same roost 82 ± 25% of the nights (mean ± sd, range = 17–100%, $n = 22$). The two females tracked during the seasons 2010/2011 and 2013/2014 used the same roost across years (Female 1: 100% fidelity in both seasons; Female 2: 100% fidelity in season 1 and 89% fidelity in season 2), whereas there was variability in the use of the roost for the female tracked across three breeding seasons (29% fidelity in season 1; 80% fidelity in season 2; 84% fidelity in season 3).

For Screaming Cowbirds, precise data were available only for the birds tagged with beeper radiotags in seasons 2010/2011 and 2011/2012. Both males and females showed 100% fidelity to their roosting site ($n = 5$ females, $n = 3$ males).

### Fidelity within a roost

Shiny Cowbird females moved on average 62.3 ± 28.8 m (mean ± sd, range = 20–102 m, $n = 15$) between nights within a roost, Screaming Cowbird females moved 57.8 ± 35.5 m (range = 16–122 m, $n = 11$) and Screaming Cowbird males moved 44.6 ± 18.9 m (range = 23–58 m, $n = 3$; see Fig. S1). The distance between opposite ends in the distribution of birds, which defined the maximum values in our simulations, were 755 and 1311 m for Shiny and Screaming Cowbirds, respectively. Monte Carlo simulations showed that movements between nights were significantly shorter than expected by chance (i.e. if the birds settled at random in the roost each night) for both Shiny (Fig. 2) and Screaming Cowbirds.
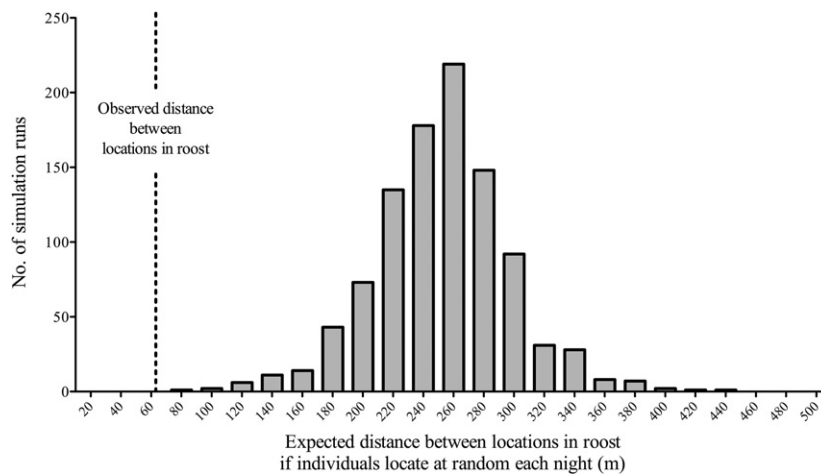
**Figure 2.** Observed mean distance between locations within the roost for a sample of 15 female Shiny Cowbirds and frequency distribution of expected observations of mean distances if females settled within the roost at random each night. The observed distance between nights falls below the 95th percentile of the distribution, indicating that females located significantly closer to the locations they used previously than expected by chance.

## Association between Screaming Cowbird pairs

Screaming Cowbird males and females that were trapped together and showed high levels of association during the day maintained their association in the roost. The three pairs tracked were recorded associated in the roost in 12/12, 11/12 and 3/4 of the records, respectively, whereas the two control 'pairs' did not show any association in any of the records (0/4 and 0/1, respectively).

## Timing of roost departures and parasitism events

Screaming Cowbird females left the roost earlier than Shiny Cowbird females (Mann–Whitney *U*-test, $U = 41.5$, $P < 0.001$, Shiny Cowbirds $n = 19$, Screaming Cowbirds $n = 11$; Table S1). Parasitic events occurred in a short time window in both species, earlier in Screaming than Shiny Cowbirds (Mann–Whitney *U*-test, $z = 4.6$, $P < 0.001$, Shiny Cowbirds $n = 21$, Screaming Cowbirds $n = 11$; Table S1).

In Shiny Cowbirds, 86% of parasitic events occurred before sunrise, with 59% of roost departures coinciding with the parasitism time window (Fig. 3a). In Screaming Cowbirds, 100% of parasitism events occurred well before sunrise and 22% of roost departures occurred during the time window of parasitism (Fig. 3b).

## DISCUSSION

We presented data on the dynamics of roost use by two species of brood parasitic cowbirds. Radio-tagging birds allowed us to analyse the individual temporal and spatial patterns of roost use. Females of both Shiny and Screaming Cowbirds mainly used a communal roost near their diurnal home-ranges throughout the breeding season. Males of Screaming, but not Shiny, Cowbirds shared the females' communal roost and pairs of Screaming Cowbirds maintained their association in the roost at night. Females of both species left the roost before and after sunrise, with a fraction of departures coinciding with the time window of parasitism. Screaming Cowbird females departed from the roost and parasitized nests earlier compared with Shiny Cowbird females.

Most radiotagged cowbirds were found roosting in large groups. Similar to other communally roosting species (reviewed by Beauchamp 1999), the benefits of roosting communally for cowbirds may include a lower predation probability (through dilution of risk, increased anti-predator vigilance or predator confusion) and higher probability of finding a mate (Bijleveld *et al.* 2010). Furthermore, Ward and Zahavi (1973) proposed that bird assemblages such as roosts could work as information centres where 'unlucky' members of the roosting community may obtain information on food location from others. In cowbirds, the possibility that females may eavesdrop, acquiring
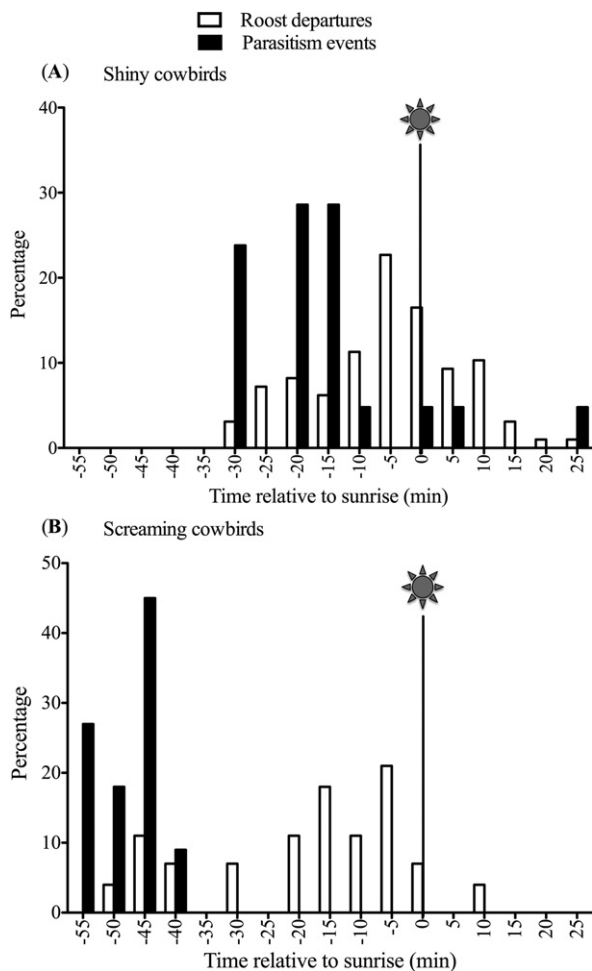
**Figure 3.** Distribution of the percentage of roost departures and parasitic events that occurred at different time intervals for Shiny Cowbird (a) and Screaming Cowbird (b) females. Shiny Cowbird roost departure times (*n* = 97) correspond to 19 Shiny Cowbird females on 1–14 different days. Shiny Cowbird parasitism events (*n* = 21) were recorded by either video-recordings or the automated telemetry system at Chalked-browed Mockingbird nests and correspond to a maximum of 18 different females (some females could not be reliably identified in video-recordings) in 20 different nests. Screaming Cowbird roost departure times (*n* = 28) correspond to 11 Screaming Cowbird females on 1–6 different days. Parasitism events (*n* = 11) were recorded by the automated telemetry system at Baywing nests and correspond to seven different females in seven different nests.

information not on feeding sites but on the location of suitable target nests, seems a likely additional benefit of roosting communally. Indirect evidence for active following has been recorded in the Shiny Cowbird, where females frequently arrive at host nests in tandems, probably due to

uninformed females 'tailing' those that fly determinedly towards a previously prospected target (Gloag *et al.* 2013). As with the foraging version of the Ward–Zahavi hypothesis, this scenario does not identify benefits for the informed animals, only for those that follow. In fact, as cowbird females typically destroy eggs before laying, being followed must be a significant liability. Identifying whether information transfer about potential host nests occurs and how the balance of costs and benefits combine to determine roosting behaviour remains a challenge for further research.

Shiny Cowbird females and Screaming Cowbirds of both sexes used roosts within close range of their diurnal home-ranges, namely the areas where they search for host nests (Scardamaglia & Reboreda 2014), and showed high levels of fidelity both between and within roosts. These findings may be related to the fact that these brood parasites must leave their roosting place and navigate towards host nests within a limited time window and in conditions of very low light intensity. Navigating from a well-known area may therefore be more beneficial than reducing the distance between roosting-site and target nest. The fact that we did not find male Shiny Cowbirds roosting in the area near their diurnal home-ranges is consistent with this idea because they do not search for or relocate host nests and consequently do not need to navigate in the dark. It is possible that Shiny Cowbird males roost near areas of higher food availability and move during the morning to areas where females search for host nests to mate. In a previous study, Scardamaglia and Reboreda (2014) showed that Shiny and Screaming Cowbird females maintain relatively stable diurnal ranges on consecutive days, which would allow females to monitor the progress of host nests and in this way synchronize their laying with that of the host. The study also provides some evidence that cowbird females fly directly from the roost to target host nests at dawn, with females having little chance of locating suitable target nests on laying days, other than by following informed females. In a related study, Scardamaglia *et al.* (2017) showed that Shiny and Screaming Cowbird females conducted prospecting visits to host nests the days before parasitism. Moreover, in this study we show that cowbird females are faithful to their nocturnal roosting sites in addition to the constant diurnal home-ranges and prospecting areas shown in previous studies (Scardamaglia & Reboreda 2014, Scardamaglia *et al.* 2017).

The strong roosting association found for pairs of Screaming Cowbirds shows that diurnal social monogamy (Scardamaglia & Reboreda 2014) extends to the roost as well. While it has been proposed that male and female Screaming Cowbirds search for and relocate nests together (Friedmann 1929, Mason 1987) because they travel in pairs throughout the day, it remains unclear whether males actively participate in these tasks or if their presence alongside females near host nests is simply the result of mate guarding. The relative enlargement of the hippocampus (an area of the brain involved in encoding spatial information; O'Keefe & Nadel 1978) in both sexes in this species, as opposed to the sex differences found between males and females in Shiny Cowbirds (Reboreda *et al.* 1996), where females search for and later relocate host nests alone, is consistent with the idea that male and female Screaming Cowbirds share the nest-searching and relocating tasks. Sharing the roost would be adaptive for Screaming Cowbird pairs if males just guard females or assist them in nest-searching and relocation. This socially monogamous mating strategy is unusual among brood parasites (Hauber & Dearborn 2003). Several hypotheses regarding avian mating systems predict that the absence of parental care should lead to an increase in numbers of mates for both females and males (Hauber & Dearborn 2003), as illustrated by the social promiscuity of Shiny Cowbirds (Mason 1987, Scardamaglia & Reboreda 2014) and also confirmed by our observations on roosting. Although the genetic mating systems still need corroboration and more information is necessary about the daily routines and copulatory behaviour of both species, it is reasonable to expect that the marked difference in mating systems is a response to differences in parasitic specialization, an aspect of mating that to our knowledge has not been explored in any detail to date.

Parasitic cowbird females, as opposed to nest-building species, are constrained to leave their roosting place and reach target nests within a limited time window, between completion of egg formation and daylight. However, on days when they do not have an egg to lay and the morning will be spent only on feeding and searching for nests, they can leave the roost later. Our data support this expectation. We found that 59% of Shiny Cowbird and 22% of Screaming Cowbird roost departures overlapped with the parasitism time window. Thus, although we cannot rule out that some roost departures that occurred during the laying time window may have not been associated with egg-laying, most departures occurring afterwards must have been non-parasitic visits or females leaving the roost to forage. The timing of departure from the roost may be a predictor of whether a female is on a laying day or not and consequently help to estimate the number of eggs laid by female cowbirds during the breeding season. The difference observed between species in the percentage of roost departures that overlap in timing with the distribution of parasitism events may be due to an underestimation of early departures by Screaming Cowbirds. Data for departures from earlier than 50 min before sunrise are missing (there are parasitic events recorded in the −55 to −50 min time bin but no roost departures were recorded for the same period or earlier). This may be attributed to the different methods that were used to record each type of event: parasitism events were recorded by automatic data-loggers in the nests that worked 24 h a day, whereas departures from the roost were recorded by a researcher with a hand-held tracking receiver in the roost area. Hence, there was a limit on the recording of times and access to roost locations, especially for Screaming Cowbirds. This leads to a potential underestimation of the percentage of departures from the roost that coincide with the parasitism time window in Screaming Cowbirds.

To summarize, we showed that throughout the breeding season, females of Shiny and Screaming Cowbirds roosted near the area in which they searched for and parasitized host nests and that the timing of roost departures can potentially predict parasitic behaviour. Our study illustrates how the use of radiotracking technologies may help understand relatively poorly known aspects of the behaviour of brood parasites.

R.C.S. collected the data, R.C.S., A.K. and J.C.R. wrote the paper, R.C.S. analysed the data.

## REFERENCES

**Adams, T.L.** 2011. *Roost site seleciton of Dunlin (Calidris alpina) on Arcata Bay, Humboldt Bay, Humboldt County, California*. M.S. Thesis. The Faculty of Humboldt State University.

**Beauchamp, G.** 1999. The evolution of communal roosting in birds: origin and secondary losses. *Behav. Ecol.* **10**: 675–687.

**Béchet, A., Giroux, J.-F., Gauthier, G. & Bélisle, M.** 2010. Why roost at the same place? Exploring short-term fidelity in staging snow geese. *Condor* **112**: 294–303.

**Bijleveld, A.I., Egas, M., van Gils, J.A. & Piersma, T.** 2010. Beyond the information centre hypothesis: communal roosting for information on food, predators, travel companions and mates? *Oikos* **119**: 277–285.

**Bivand, R. & Rundel, C.** 2016. *rgeos: Interface to Geometry Engine - Open Source (GEOS)*. R package version 0.3-20. [Online.] Available at: https://cran.r-project.org/package=rgeos (accessed 20 February 2017).

**Conklin, J.R.J., Colwell, M.A. & Lank, D.B.** 2007. Diurnal and nocturnal roost site fidelity of Dunlin (*Calidris alpina pacifica*) at Humboldt Bay, California. *Auk* **124**: 677–689.

**Cruz, A., Manolis, T. & Andrews, R.** 1990. Reproductive interactions of the Shiny Cowbird *Molothrus bonariensis* and the Yellow-hooded Blackbird *Agelaius icterocephalus* in Trinidad. *Ibis* **132**: 436–444.

**De Mársico, M.C., Mahler, B., Chomnalez, M., Di Giácomo, A. & Reboreda, J.C.** 2010. Host use by generalist and specialist brood-parasitic cowbirds at population and individual levels. *Adv. Study Behav.* **42**: 83–121.

**Dhondt, A.A., Driscoll, M.J.L. & Swarthout, E.C.H.** 2006. House Finch *Carpodacus mexicanus* roosting behaviour during the non-breeding season and possible effects of Mycoplasmal conjunctivitis. *Ibis* **149**: 1–9.

**Feare, C. & Zaccagnini, M.** 1993. Roost departure by Shiny Cowbirds (*Molothrus bonariensis*). *Hornero* **13**: 292–293.

**Fiorini, V.D. & Reboreda, J.C.** 2006. Cues used by Shiny Cowbirds (*Molothrus bonariensis*) to locate and parasitise Chalk-browed Mockingbird (*Mimus saturninus*) nests. *Behav. Ecol. Sociobiol.* **60**: 379–385.

**Fraga, R.M.** 1985. Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. *Ornithol. Monogr.* **36**: 829–844.

**Fraga, R.M.** 1991. The social system of a communal breeder, the Bay-winged Cowbird *Molothrus badius*. *Ethology* **89**: 195–210.

**Fraga, R.M.** 1998. Interactions of the parasitic Screaming and Shiny Cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the Bay-winged Cowbird (*M. badius*). In Rothstein, S.I. & Robinson, S.K. (eds) *Parasitic Birds and Their Hosts. Studies in Coevolution*: 173–193. New York, NY: Oxford University Press.

**Friedmann, H.** 1929. *The Cowbirds. A Study in the Biology of Social Parasitism*: 57–144. Springfield, IL: C. Thomas.

**Gates, J.E. & Evans, D.R.** 1998. Cowbirds breeding in the Central Appalachians: spatial and temporal patterns and habitat selection. *Ecol. Appl.* **8**: 27–40.

**Gloag, R., Fiorini, V.D., Reboreda, J.C. & Kacelnik, A.** 2012. Brood parasite eggs enhance egg survivorship in a multiply parasitized host. *Proc. R. Soc. B* **279**: 1831–1839.

**Gloag, R., Fiorini, V.D., Reboreda, J.C. & Kacelnik, A.** 2013. The wages of violence: mobbing by mockingbirds as a frontline defence against brood-parasitic cowbirds. *Anim. Behav.* **86**: 1023–1029.

**Hahn, D., Sedgwick, J., Painter, I. & Casna, N.** 1999. A spatial and genetic analysis of cowbird host selection. *Stud. Avian Biol.* **18**: 204–217.

**Hauber, M.E. & Dearborn, D.C.** 2003. Parentage without parental care: what to look for in genetic studies of obligate brood-parasitic mating systems. *Auk* **120**: 1–13.

**Hoy, G. & Ottow, J.** 1964. Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. *Auk* **81**: 186–203.

**Kattan, G.H., Posada, A., Arenas, D.F., Moreno, J.L. & Barrera, Á.** 2016. Flocking behavior of Shiny Cowbirds (*Molothrus bonariensis*) at feeding areas during the daily cycle. *Wilson J. Ornithol.* **128**: 441–445.

**Laughlin, A.J., Sheldon, D.R., Winkler, D.W. & Taylor, C.M.** 2014. Behavioral drivers of communal roosting in a songbird: a combined theoretical and empirical approach. *Behav. Ecol.* **25**: 734–743.

**Mason, P.** 1980. *Ecological and evolutionary aspects of host selection in cowbirds*. D. Biol. Thesis, University of Texas, Austin.

**Mason, P.** 1987. Pair formation in cowbirds: evidence found for Screaming but not Shiny Cowbirds. *Condor* **89**: 349–356.

**Morrison, D.W. & Caccamise, D.F.** 1985. Ephemeral roosts and stable patches – A radiotelemetry study of communally roosting Starlings. *Auk* **102**: 793–804.

**Morrison, D.W. & Caccamise, D.F.** 1990. Comparison of roost use by three species of communal roostmates. *Condor* **92**: 405–412.

**O'Keefe, J. & Nadel, L.** 1978. *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.

**Paquet, M., Doutrelant, C., Loubon, M., Theron, F., Rat, M. & Covas, R.** 2016. Communal roosting, thermoregulatory benefits and breeding group size predictability in cooperatively breeding sociable weavers. *J. Avian Biol.* **47**: 749–755.

**du Plessis, M.A., Weathers, W.W. & Koenig, W.D.** 1994. Energetic benefits of communal roosting by Acorn Woodpeckers during the nonbreeding season. *Condor* **96**: 631–637.

**R Core Team** 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available at: https://www.r-project.org/ (accessed 20 February 2017).

**Rappole, J.H. & Tipton, A.R.** 1991. New harness design for attachment of radio transmitters to small passerines. *J. Field Ornithol.* **62**: 335–337.

**Reboreda, J.C., Clayton, N. & Kacelnik, A.** 1996. Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *NeuroReport* **7**: 505–508.

**Scardamaglia, R.C. & Reboreda, J.C.** 2014. Ranging behavior of female and male Shiny Cowbirds and Screaming Cowbirds while searching for host nests. *Auk* **131**: 610–618.

**Scardamaglia, R.C., Fiorini, V.D., Kacelnik, A. & Reboreda, J.C.** 2017. Planning host exploitation through prospecting visits by parasitic cowbirds. *Behav. Ecol. Sociobiol.* **71**: 23.

**Thompson, F.** 1994. Temporal and spatial patterns of breeding Brown-headed Cowbirds in the midwestern United States. *Auk* **111**: 979–990.

**Tuero, D.T., Fiorini, V.D. & Reboreda, J.C.** 2007. Effects of Shiny Cowbird parasitism on different components of House Wren reproductive success. *Ibis* **149**: 521–527.

**Ursino, C.A., De Mársico, M.C., Sued, M., Farall, A. & Reboreda, J.C.** 2011. Brood parasitism disproportionately increases nest provisioning and helper recruitment in a cooperatively breeding bird. *Behav. Ecol. Sociobiol.* **65**: 2279–2286.

**Ward, P. & Zahavi, A.** 1973. The importance of certain assemblages of birds as 'information-centres' for food-finding. *Ibis* **115**: 517–534.

**Weatherhead, P.J.** 1987. Field tests of information transfer in communally roosting birds. *Anim. Behav.* **35**: 614–615.

**White, G.C. & Garrott, R.A.** 1990. Estimating animal locations. In *Analysis of Wildlife Radio-Tracking Data*: 41–78. San Diego, CA: Academic Press.

**Winkler, D.W.** 2006. Roosts and migrations of swallows. *Hornero* **21**: 85–97.

**Yom-Tov, Y.** 1979. The disadvantage of low positions in colonial roosts: an experiment to test the effect of droppings on plumage quality. *Ibis* **121**: 331–333.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Detailed methods and analysis**. Comparison between tagging methods, fidelity within a roost analysis and simulation.

**Figure S1**. Spatial fidelity within roosts for (a) Shiny Cowbird females and (b) Screaming Cowbird females (F) and males (M) monitored during four or more nights during the breeding season.

**Table S1**. Times of departures and parasitic events for Shiny and Screaming Cowbirds.