Out on their own: a test of adult-assisted dispersal in fledgling brood parasites reveals solitary departures from hosts

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Brood-parasitic offspring sexually (mis)imprinting on the foster parents is considered one of the greatest constraints to the evolution of interspecific avian brood parasitism. While most nonparasitic juvenile birds learn the behaviours and mate choice preferences from their own parents, social parasites must avoid misimprinting on their host species' phenotype in order to accurately recognize conspecifics. One possible mechanism to assure accurate species recognition by juvenile parasites is to begin to associate with adult parasitic conspecifics, known as the 'first contact' scenario, whereby adult female parasites facilitate the dispersal of their offspring away from hosts, thus providing accurate referents for conspecific recognition. Using an automated radiotelemetry system, we determined the presence or absence (every 1–2 min during three breeding seasons; 516 315 search occasions) of radiotagged parasitic adult female brown-headed cowbirds, *Molothrus ater*, and compared their departures from a forest study site with those of genetic offspring or experimentally transplanted (nonrelated) juvenile cowbirds within the female's egg-laying range. Contrary to our predictions, we found no support for the facilitation of juvenile cowbird dispersal by adult female cowbirds. Juvenile cowbirds typically were not located within their mother's home range when departing the forest and, likewise, departure events for natal and experimentally transplanted juveniles (<2%) did not overlap temporally with the departure of the genetically assigned mother or with the departure of other local radiotagged female cowbirds. Surprisingly, we found that juvenile cowbirds primarily departed from the host's territory at sunset, when adult female cowbirds are infrequently present within the forest. Our results suggest that the solitary nocturnal roosting behaviour of juvenile cowbirds may facilitate independence from their hosts, thus minimizing the risk of misimprinting on heterospecific phenotypes. This strategy may also indirectly promote conspecific interactions, providing further evidence for the importance of independent spatial and social preferences of hosts and brood parasites in the evolution of avian brood parasitism.

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Interspecific avian brood parasites exploit the parental care of host species and avoid the energetic demands of raising offspring by laying their eggs in host species' nests. Obligate brood parasitism has served as a 'model system' influencing our understanding of both the coevolutionary process (Feeney, Welbergen, & Langmore, 2014; Rothstein, 1990; Soler, 2014) and the social recognition systems (Göth & Hauber, 2004) of hosts and parasites. Similarly, with opportunities to readily quantify the costs and benefits of this intriguing form of reproduction, avian host–parasite systems provide an opportunity to understand some constraints on the evolution of life-history strategies, including parental investment (Kruger, 2007).

Obligate avian brood parasitism has proven to be a persistent reproductive strategy, having evolved independently at least seven times from nonparasitic, parental ancestors (Rothstein, 1990; Yom-Tov & Geffen, 2006). Yet brood parasitism is rare (~1 % of all bird species; Payne, 1977), probably reflecting the constraints that arise during the initial evolution of interspecific brood-parasitic behaviours. In nearly every test where the offspring of two bird species are switched early in the nestling phase, cross-fostered juveniles learn the behaviours and mate choice decisions of their foster species (i.e.

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sexual imprinting: ten Cate & Vos, 1999), including facultative interspecific parasites (Sorenson, Hauber, & Derrickson, 2010). While sexual imprinting has significant implications for speciation by influencing the recognition process of suitable mates in many sexually reproducing species (Irwin & Price, 1999; Laland, 1994), including African brood parasites (Payne, Payne, Woods, & Sorenson, 2000), sexual imprinting is conversely one of the greatest constraints on the evolution of brood parasitism (Davies, 2000; Slagsvold & Hansen, 2001; Sorenson et al., 2010). This leads to the question of how juvenile brood parasites avoid sexually misimprinting on their host species (Hauber, Russo, & Sherman, 2001).

Misimprinting would result in hybridization between hosts and parasites; yet, hybridization is rarely documented within the ~100 species of extant obligate brood parasites (e.g. Payne & Sorenson, 2004). While genetically based preferences for conspecific phenotypes probably guide species recognition, learning strongly contributes to recognition systems in both parasitic and nonparasitic bird species (Hauber et al., 2001; Payne et al., 2000; Price, 2008). When raised in isolation, the obligate brood-parasitic brown-headed cowbird, *Molothrus ater*, responds with copulatory displays to conspecific song (King & West, 1977), and even as nestlings, increases begging in response to conspecific calls (Hauber et al., 2001), indicating the earliest onset of conspecific recognition capabilities. Yet, by experimentally extending social contact with heterospecific species in aviaries, both male cowbirds and redheads, *Aythya americana* (a facultative interspecific parasitic duck), prefer to sexually display to their hosts over conspecifics (Freeberg, King, & West, 1995; Sorenson et al., 2010). Thus, laboratory experimentation has revealed a species recognition paradox, whereby brood parasites incorporate learned phenotypic components for conspecific recognition and mate choice, in spite of being raised by inappropriate referents (i.e. their host species; Göth & Hauber, 2004). However, by spatially segregating from the host prior to critical periods for song learning and mate choice, typical in the development of young songbirds (Bateson, 1979; Brainard & Doupe, 2002; Hensch, 2004), juvenile brood parasites could avoid sexually imprinting on their host. Here we set out to test this hypothesis of early spatial segregation from the host by juveniles of an obligate brood parasite.

Adult brood parasites are generally thought to relinquish all forms of parental care after laying their eggs, but adult parasites could influence the dispersal of their offspring away from their hosts ('first contact' hypothesis; Hauber, 2002). The guidance of juvenile brood parasites away from hosts would not only reduce the chance of misimprinting, but the interaction with the adult cowbird would directly provide salient conspecific songs and behaviours suitable for appropriate sexual imprinting and survival. Female-assisted dispersal of offspring provides a mechanism to explain why Hahn and Fleischer (1995) reported that 36% of adult female–juvenile cowbird pairs captured while feeding together were closely related. Similarly, some evidence indicates that juvenile brood-parasitic great spotted cuckoos, *Clamator glandarius*, potentially learn to recognize conspecifics by imprinting on adult cuckoos that have maintained contact throughout the nestling and fledgling period (Soler & Soler, 1999). Adult female brood parasites may have played an important role in the evolution of brood parasitism by facilitating postfledging dispersal and initiating species recognition in their own offspring, thereby circumventing the constraint of sexually imprinting on the host species (Hauber & Dearborn, 2003). Critically, the juvenile parasitic spatial segregation from hosts and the conspecifically assisted avoidance of sexual misimprinting hypotheses make specific predictions about the social developmental trajectory of brood parasitic young, which can be tested by extensively tracking the location of juvenile and adult parasites in space and time.

We used an automated radiotelemetry system (ARTS), where the study site occupancy of female brown-headed cowbirds and their offspring could be estimated every 1–2 min, to investigate whether adult females facilitate the departure of juvenile cowbirds from their hosts. Adult female cowbirds preferentially approach conspecific juveniles in the laboratory and conspecific calls broadcast in the wild, over heterospecifics (Hauber, 2002), and likewise, juvenile cowbirds prefer to associate spatially with adult conspecific female calls over heterospecific calls in laboratory (Hauber, 2002) and in field choice trials (Hauber et al., 2001), providing support for the hypothesis of female-assisted departure of their offspring. Adult female cowbirds are typically spatially faithful to a breeding area throughout the season (Dufty, 1982; Hahn, Sedgwick, Painter, & Casna, 1999; Hauber, Strausberger, Feldheim, Lock, & Cassey, 2012; Raim, 2000; Rivers et al., 2012) and monitor the content of recently parasitized nests (Hoover & Robinson, 2007), further presenting female cowbirds with the opportunity to facilitate the necessary dispersal of juvenile cowbirds. We predicted that (1) juvenile cowbirds would be located within their mother's home range after they departed from their host's nest and (2) juvenile departures would coincide with their mother's movement away from the host. We further predicted that departure events of juvenile cowbirds experimentally transplanted within a different female's home range would correlate with the departure times of the local female, suggestive of conspecific bias in juvenile cowbirds' following behaviours. We also investigated general patterns of juvenile departure events and female study site occupancy to determine whether juvenile dispersal is guided by nonrelated females.

METHODS

Species and Study System

We studied the movements of brown-headed cowbirds during four breeding seasons within a long-term (20+ years) nestbox study system located within the Cache River watershed, southern Illinois U.S.A., which facilitates investigations of the host–parasite interactions between prothonotary warblers, *Protonotaria citrea*, and brown-headed cowbirds (e.g. Hoover, 2003). The prothonotary warbler, a Neotropical migratory songbird that breeds in bottomland swamps throughout the southeastern United States, is the only frequent cowbird host species that nests in artificial nestboxes (Petit, 1999). Adult brown-headed cowbirds forage socially in pastures and agriculture, and female cowbirds subsequently parasitize the songbirds within the surrounding landscape (Thompson, 1994), particularly forests (Hahn & Hatfield, 1995).

The warblers are able to raise cowbird nestlings successfully (Hoover, 2003) and their nestboxes are commonly parasitized (~70%; Hoover & Hauber, 2007; Hoover, Yasukawa, & Hauber, 2006). We placed nestboxes 50–100 m apart within suitable habitat on greased conduit poles, and upon hatching, surrounded the nestbox with wire to eliminate the chance for nest predation. To reduce the effects of nest ectoparasites, such as bird blowfly maggots (*Protocalliphora* spp.) on nestling and fledgling survival (e.g. Streby, Peterson, & Kapfer, 2009), we replaced the nesting material every 3–5 days with Spanish moss after hatching. Each active nestbox was checked every 1–2 days during the egg-laying stage and then monitored every 3–5 days until fledging. Most cowbird chicks are raised in the absence of conspecifics (Hauber, 2001; Lowther, 1993); however, occasionally more than one cowbird is raised in a brood (e.g. Hoover, 2003; McLaren, Woolfenden, Gibbs, & Sealy, 2003; Rivers et al., 2012). Being raised with cowbird nestmates could theoretically impact the recognition system (Soler & Soler, 1999); therefore, we limited each parasitized nest to a single cowbird nestling (labelled 'natal' nestbox/chick hereafter).

We experimentally added a single cowbird nestling (labelled 'transplanted' hereafter), collected more than 1 km from the study sites, to nonparasitized warbler nests and to parasitized nests that failed to hatch cowbird offspring. In multiply parasitized nests where more than cowbird nestling hatched, we moved the additional cowbird nestlings (1—4 days posthatching) to a nestbox on a different study site with appropriately aged nonparasitized nests or where cowbird eggs had failed to hatch.

Radiotelemetry

During 2011—2014, we captured adult female cowbirds within the study sites by broadcasting cowbird calls adjacent to a mist net or by inserting trap doors within active warbler nestboxes prior to cowbird egg laying in the early morning (1 h before sunrise); we then removed the trap doors after the cowbird's capture and prior to the warbler's egg laying. Adult female cowbirds were captured during the first weeks of egg laying within our study site and prior to fledging of the juveniles. We attached radiotransmitters to adult female and juvenile cowbirds (transmitter mass = 1.6 and 0.9 g, respectively; <5% body mass) within two distinct study sites (ABC and HB, separated by ~1 km; Fig. 1).

Using the figure-8 harness method (Rappole & Tipton, 1991), transmitters were positioned on the cowbird's lower back and held in place using an elastic nylon beading cord that looped around each thigh. Harnesses were made in advance to minimize handling time, and nylon was chosen as it deteriorates over time and will fall off the individual (~3—6 months; Streby et al., 2015). We attached transmitters to juvenile cowbirds on the morning of posthatch day 10, the mean age of fledging (Woodward, 1983). Using a handheld three-element Yagi antennae and receiver, we searched for each

Figure 1. Aerial view of the study system depicting the locations of each site (ABC and HB; grey polygons), the automated radiotelemetry system (ARTS) towers (stars), the baited fly-in trap (denoted by an X). The study site HB was within the ARTS coverage.

cowbird within the study sites throughout the transmitter life span (adult transmitter: ~12 weeks; juvenile transmitter: 3—5 weeks; Holohil Systems Ltd, Carp, ON, Canada; JDJC Corp., Fisher, IL, U.S.A.), or until the cowbird was not detected for 5 days. We identified locations for radiotagged individuals within the forest by visual detection, or when not observed due to dense vegetation, we inferred the location based on the strength of the telemetry signal at several angles from the suspected location. We did not detect any additional noticeable stress or mortality caused by radiotelemetry on juveniles or adult females. Locations determined by radio-tracking were recorded using a hand-held global positioning system receiver (GPS 3, Garmin, Olathe, KS, U.S.A.). We estimated the distance (m) of each juvenile cowbird's location from its fledging nestbox (Euclidean straight-line). Radiotelemetry and sampling of brown-headed cowbirds was approved by the University of Illinois Institutional Animal Care and Use Committee (permit numbers: 09107, 12079 and 12080), the U.S. Fish and Wildlife Service (permit number: MB815400-0) and the U.S. Geological Survey (banding permit number: 06507).

We liberally estimated forest home ranges for female cowbirds based on 100% minimum convex polygons (MCP), the smallest polygon that encompasses all recorded radiotracked locations for each female within the forest for a given year. As opposed to home range estimation techniques such as kernel estimators, MCPs have the tendency to overestimate home range size (Powell, 2000), because the polygon probably includes areas seldom used by the animal. However, we think that MCPs provides the best test of our hypothesis for the potential area of overlap where juveniles have the greatest potential to encounter the female cowbird in question. If, in turn, our hypothesis is not supported, we provide a very conservative test.

Automated Radiotelemetry System

To estimate the timing of adult and juvenile cowbird's occupancy and departure from the study sites, we deployed an automated radiotelemetry system in 2012 (ARTS; Kays et al., 2011; Ward, Alessi, Benson, & Chiavacci, 2014; Ward, Sperry, & Weatherhead, 2013). We placed three towers in association with one study site (HB; Fig. 1): two tall towers (18 m) placed to the north/south borders and one short tower (5 m) positioned within the study site. Each tower held six directional antennas, spaced by 60°, to give 360° coverage and an automated recording unit (ARU; JDJC Corp.), which systematically recorded the signal strength (in dBm) for individual radio frequencies programmed at ~1—2 min intervals. To quantify study site occupancy, we derived signal strength thresholds, where an individual was considered present within the forest if the signal strength was greater than −130 dBm (0.1 fW) for any south antennas (120° and 180°) for tower 1, any north antennas (0°, 60° and 300°) for tower 2 and any antenna on tower 3. This signal strength threshold was derived from comparisons of signal strength of radiotagged juveniles and adults that were known to occur within the forest from hand-tracked observations. This threshold was also considered conservative in that relatively weak transmitter signals detected by the ARTS, from individuals either sitting on the ground or making short-distance departures, would be considered present within the forest under this criterion. To account for electromagnetic noise, which can obscure occupancy data from apparent signals that appear to be from the radiotransmitter, we estimated noise by measuring the signal strength between transmitter pulses, and we dismissed the data when noise was greater than −130 dBM (0.1 fW).

We pooled binomial (yes/no) occupancy data into 30 min intervals for analysis, and individuals were considered present within the forest if detected more than two times during a given interval.

We assumed that an individual left the forest if it was not detected in the subsequent 30 min interval. In other words, we classified departure events when individuals transitioned from present to absent for at least 30 min. Intervals with fewer than three observations, typically due to electromagnetic noise from lighting, were removed from the analysis. For analysis and presentation, we grouped time observations into distinct groups: sunrise = 1.5 h buffer around sunrise (0400–0700 hours); morning = 0700–1200 hours; afternoon = 1200–1830 hours; sunset = 1.5 h buffer around sunset (1830–2130 hours); night = 2130–0400 hours. To determine the reliability of ARU-detected occurrence and departure events, we compared the presence/absence data with known occurrences within the forest determined by hand-tracked locations.

Maternity Analysis

To determine maternity of natal and transplanted radiotracked juveniles, we collected blood samples with sterile needles (~50 μl) from the brachial vein of juvenile and adult cowbirds, both males and females, captured within the forest and at a feeder trap (see below), and stored the samples in lysis buffer at ambient temperatures or at 4 °C. We used DNeasy Blood and Tissue kit (Qiagen, Valencia, CA, U.S.A.) to extract DNA from all blood samples. We did not observe any significant harm (e.g. infection, excessive clotting) caused by the collection of blood samples. We used nine microsatellite primer pairs for genotyping and followed PCR amplification described in previous studies: three loci (CB 1, CB 12 and CB 15) described in Longmire et al. (2001), three loci (Maμ 10, Maμ 25 and Maμ 29) described in Alderson, Gibbs, and Sealy (1999), two loci (Maμ 101 and Maμ 104) described in Strausberger and Ashley (2001) and one (Maμ 102) described in Strausberger and Ashley (2003). The forward primer for each locus was fluorescently labelled (6-FAM, HEX, or NED) and analysed on an AB 3730xl DNA analyzer (Biotechnology Center, University of Illinois, Urbana, IL, U.S.A.) to determine fragment sizes. Genotypes were assigned, both manually and automatically, using GeneMapper 3.7 (Applied Biosystems, Foster City, CA, U.S.A.).

Deviations from Hardy–Weinberg equilibrium (HWE) of the nine microsatellite loci were tested using Genepop'007 (Rousset, 2008). For maternity analysis, we used a likelihood-based approach implemented in CERVUS 3.0 (Kalinowski, Taper, & Marshall, 2007) to assign genotyped mothers to their putative offspring. Because parentage assignment in CERVUS depends largely on the genetic variability of the loci used and their resulting power to exclude potential parents, we attempted to increase the accuracy of allele frequencies for the study population by including the genotypes of male and female cowbirds captured at a feeder trap in addition to the adults captured within the study sites. The fly-in trap, located ~1 km from the study sites (Fig. 1), was baited with a corn–sunflower seed mixture and watched continually during trapping attempts. To determine the statistical confidence of maternity assignments, we performed a simulation of 10 000 tests based on observed genotype frequencies, assuming 90% of candidate mothers were sampled, a breeding population of 20 adult females among the study sites and 0.01 error rate for all loci. Maternal identity to radiotagged juveniles was assigned with ≥95% confidence, as determined by the likelihood-odds ratios (Kalinowski et al., 2007).

Statistical Analyses

We used a linear mixed-effect model (LMM) to determine whether the distance (m; response variable) from the natal or transplanted box was influenced by postfledging age. To determine whether the duration of time spent out of the forest after a departure event varied throughout the day, we used a LMM and included time interval (sunrise, morning, afternoon, sunset and night) as an explanatory variable and the time after departure as the response variable. Because the duration of time and distance tended to be right-skewed, we used an exponential response distribution; results were qualitatively similar when compared to log-transformed response variables. For binary response variables, we used generalized linear mixed models (GLMM) with a binomial response, logit link function, and Laplace likelihood approximation (Bolker et al., 2009). We included whether the juvenile's hand-tracked location was inside the respective female's home range (binomial response variable) with postfledging age as an explanatory variable. To analyse the probability of juvenile departure (binomial response), we included time interval. Similarly, we included time interval as an explanatory variable to predict the probability of forest occupancy for adult females (binomial response). We included only those juveniles that were continually located for more than 10 days postfledging, assuming that cowbirds disperse from their natal site 20–30 days after fledging (Woodward, 1983). Juvenile models included whether or not the individual was transplanted (categorical) as an explanatory variable. Our data included only adult females that were present within the forest at least once on a given day; thus, we were unable to analyse seasonal occupancy data for adult females. All models included animal identity as a random effect to account for potential issues associated with pseudoreplication. All statistical analyses were performed in SAS 9.4 (SAS Institute, Cary, NC, U.S.A.) and parameter estimates are presented with ± 95% confidence intervals (CI) or standard errors (SE).

RESULTS

Maternity

We included the microsatellite genotypes of 101 known adults (54 females, 47 males) captured within and adjacent to the nestbox study sites for maximum likelihood simulations and to estimate confidence of maternity assignments. The allelic frequencies for each loci were in HWE (chi-square test: all $\chi^2 < 4.41$, $P > 0.11$), with the exception of CB 1 ($\chi^2 = 13.29$, $P < 0.01$). Therefore, we eliminated CB 1 from maternity assignment analyses. We included all 54 females as candidate mothers for radiotagged juvenile cowbirds. Of the 15 radiotagged juveniles reared in their natal nestbox, we assigned nine (60%) to a radiotagged mother for the given year and two to female cowbirds captured in subsequent years. The radiotagged transplanted juveniles ($N = 5$) were not assigned to any local females.

Forest Locations

We recorded locations for juveniles every 1–2 days (mean ± SE = 17 ± 0.08 locations per postfledging) to determine the effects of age on the distance juveniles travelled from their natal nest. Results from a LMM indicated that juveniles ($N = 20$) were located at greater distances from the fledging nestbox with increasing postfledging age (LMM: $\beta \pm SE = 0.13 \pm 0.01$, $N = 345$; $F_{1,324} = 190.93$, $P < 0.001$; Fig. 2), and there was no difference in mean distance between transplanted ($N = 5$) and natal ($N = 15$) juveniles ($F_{1,324} = 0.61$, $P = 0.44$).

To determine the likelihood that juveniles would come into contact with their genetic mothers or other radiotagged female cowbirds (for transplanted juveniles), we calculated the MCP as an estimate of the home range for each female cowbird. Within the two study sites, we captured and radiotagged 15 adult females, of which three were radiotagged in multiple years. One juvenile cowbird was transplanted into an area lacking a radiotagged female
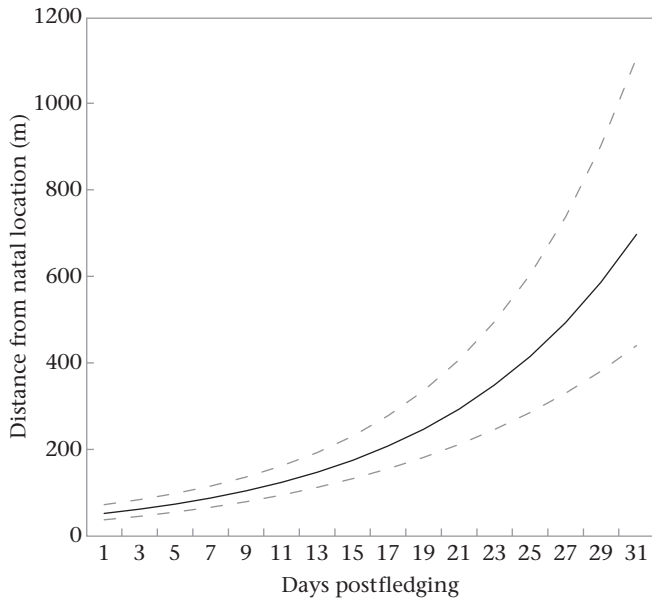
Figure 2. Relationship between the distance of radiotracked locations from the natal nestbox and the postfledging age of juvenile cowbirds ($N = 20$). Mean predicted distance ($\pm$95% CI) for a given postfledging age shown from results of a LMM ($N = 345$ locations) with an exponential response distribution; animal identity was included as a random effect.

cowbird and was removed from this analysis. We found that both transplanted juveniles ($N = 4$) and natal juveniles assigned to a radiotagged mother ($N = 9$) were more likely to be located outside of their respective female's home range with increasing postfledging age (GLMM: $\beta \pm$ SE $= -0.16 \pm 0.03$, $N = 220$; $F_{1,206} = 30.97$, $P < 0.001$; Fig. 3), and that the mean probabilities of being outside the foster/natal nest female's home range did not differ for transplanted and natal juveniles ($F_{1,206} = 0.05$, $P = 0.83$).
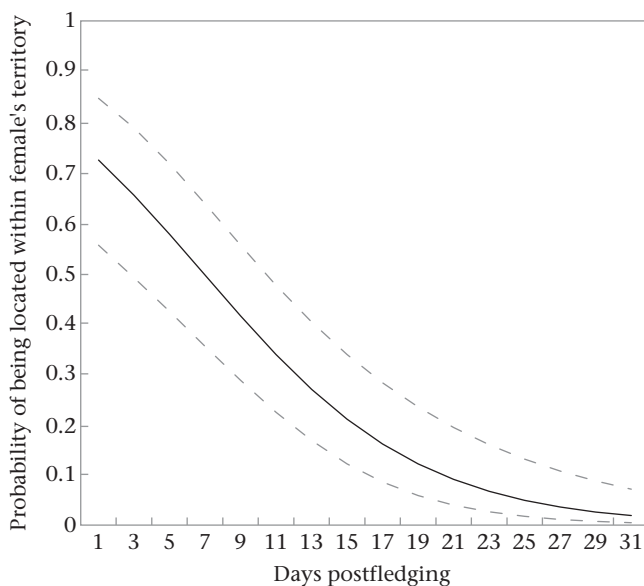
Forest Occupancy and Departure

To determine the probability of forest occupancy and identify departures from the forest, we used data collected from the ARTS during the summers of 2012–2014 within a single study site (HB: Fig. 1) bordered by radiotelemetry towers. The ARTS recorded the signal strength for adult female and juvenile radio frequencies on 516 315 occasions with 227 665 identified detections (> -130 dBm; 0.1 fW). Data were binned into 30 min intervals ($N = 23\,925$) and the ARTS 'searched' for the given transmitter every 1–2 min (mean $= 21.2$ times per 30 min period). By comparing the observations collected via hand tracking adult and juvenile cowbirds ($N = 327$), only three observations (1%) were discordant with the occupancy data; in each case the recorded times may have conflicted between the hand-tracked and ARTS data as occupancy was detected by the ARTS about 10 min after the recorded hand-tracked observation. Therefore, the occupancy estimations derived from the ARTS data appear reliable.

We tracked 10 juveniles with ARTS for the 7296 time intervals, of which, we identified juveniles to be present within the forest on 6718 (92%) intervals. Adult females ($N = 11$) were present in the forest 40% of the 16 629 time intervals available for detection. Assuming that a lack of detection for at least 30 min subsequent to being detected represents a departure from the forest, we identified 58 departure events for juvenile cowbirds (range 0–16 per individual). The probability of detecting at least one departure event increased with postfledging age (GLMM: $\beta \pm$ SE $= 0.25 \pm 0.04$, $N = 163$; $F_{1,152} = 34.28$, $P < 0.001$; Fig. 4) and there was no difference between transplanted and natal juveniles ($F_{1,152} = 0.17$, $P = 0.83$). The probability that a juvenile left the forest varied throughout the day (GLMM: $F_{4,773} = 6.55$, $N = 787$, $P < 0.001$; Fig. 5a). Juvenile departures were most likely to occur (mean $\pm$ SE $= 0.11 \pm 0.04$) within 1.5 h of sunset (1830–2130 hours), twice the likelihood of afternoon mean departure probability (mean $\pm$ SE $= 0.05 \pm 0.02$). The probability of occurrence within the forest for adult female cowbirds varied throughout the day (GLMM: $F_{4,1431} = 123.12$, $N = 1443$, $P < 0.001$; Fig. 5b). Yet, we found the probability of occurrence for adult females to be relatively low (mean $\pm$ SE $= 0.20 \pm 0.04$) within 1.5 h of sunset, indicating that most juvenile departure events took place when females were unlikely to be present within the forest.
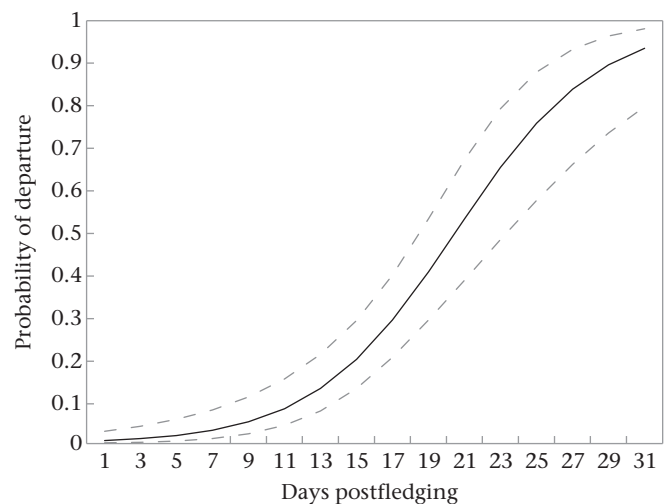

Figure 3. Probability of a radiotagged juvenile cowbird ($N = 9$) being located within its maternal, or when transplanted, the local female cowbird's home range relative to the juvenile's postfledging age. Predicted probabilities presented ($\pm$95% CI) from a GLMM ($N = 220$ juvenile locations), with animal identity included as a random effect.

Figure 4. Probability of departure (detected by ARTS) from the forest by radiotagged juvenile cowbirds ($N = 10$) relative to their postfledging age. Predicted probabilities presented ($\pm$95% CI) from a GLMM ($N = 163$ observation days), with animal identity included as a random effect.
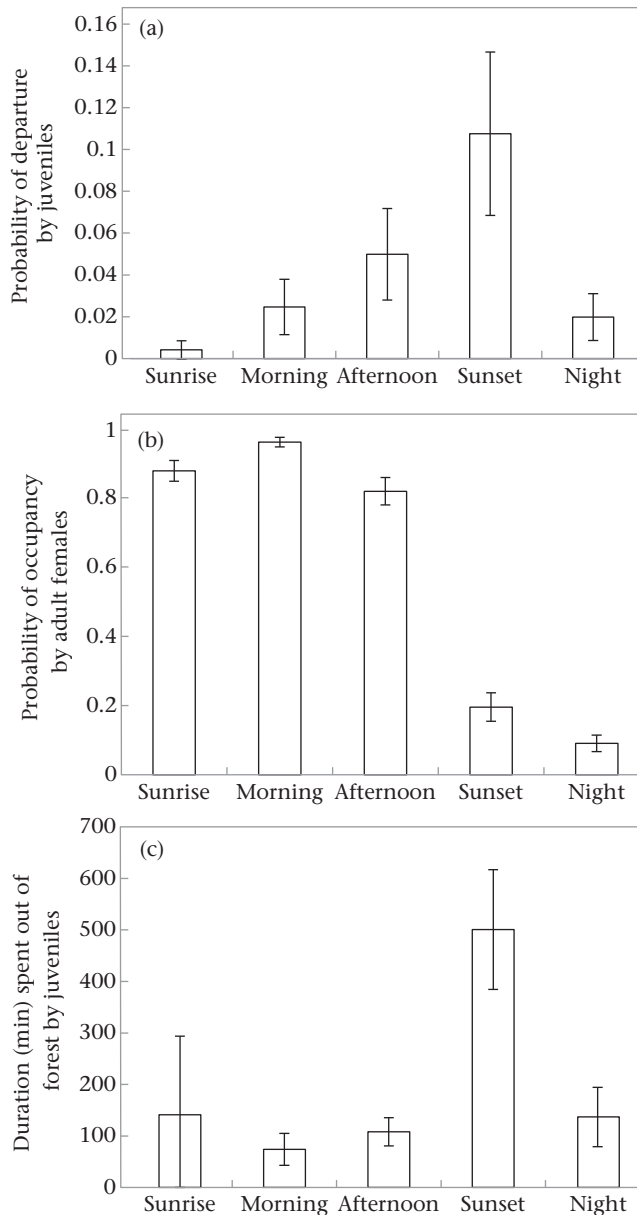
Figure 5. (a) Probability of forest departure for juvenile cowbirds ($N = 787$ observations). (b) Probability of forest occupancy for eight adult female cowbirds ($N = 1443$ observations) in relation to time intervals. (c) Duration (min) of absence during excursions outside of the forest for juvenile cowbirds ($N = 54$ departures) and time of day. Predicted probabilities ($\pm$SE) are presented from results of GLMMs while including animal identity as a random effect.

The duration that juveniles were not detected within the forest varied among time periods (GLMM: $F_{4,43} = 19.30$, $N = 54$, $P < 0.001$; Fig. 5c), and the average duration was greatest following sunset departure events (mean $\pm$ SE $= 500 \pm 116$ min). In concordance with the departure events detected by ARTS, we documented three radiotagged juveniles (range 20–30 days postfledge) departing the forest while hand tracking within 1 h of sunset. We were able to locate the destination for two of these juveniles, each roosting in grassy fields 0.1–0.5 km from the forest for a total of 7 evenings. On both occasions, we did not observe any warbler host or other cowbirds in proximity to the recently departed juveniles. All three juveniles were observed within the forest the following morning, near their initial departure locations and receiving

parental care from their hosts. We located two additional radiotagged juveniles about 1 km outside of the HB study site during the afternoon, and each subsequently returned to its host parents within the forest, but we were unable to determine whether any juvenile or adult cowbirds accompanied the two juveniles during their departures.

Temporal Correlation in Departure Events

Of the 58 juvenile departure events identified by ARTS, 35 (70%) occurred on days when the assigned radiotagged mother, or associated female for transplanted juveniles, was detected within the forest. We found a negative correlation between the time of juvenile dispersal and the presence of the associated female cowbird (logistic regression: $\beta \pm$ SE $= -0.78 \pm 0.36$, $N = 35$; $\chi^2 = 4.39$, $P = 0.03$), with only 14 (31%) juvenile departures occurring at times when the associated female was present within the forest. Indeed, we only detected four (6.8%) juvenile departure events occurring during the same 30 min interval as when any radiotagged adult female cowbird was detected departing the forest. We detected one juvenile departure event that overlapped with the departure of the genetically assigned mother, yet there were 24 min separating the specific departure times as determined by raw (i.e. not binned into 30 min periods) ARTS data. The three additional temporally correlated departure events were those of transplanted juveniles, each coinciding with the departure of radiotagged female cowbirds whose home range did not include the respective transplanted juvenile. In addition, we identified a single pair of juveniles that departed during the same time interval, each located outside of their respective female's home range and located back within the forest on the following morning. Although our study design prohibited an accurate estimate for the random co-occurrence of juvenile female departures, juvenile departures rarely overlapped with any female, and we directly observed juveniles dispersing solitarily; thus, we concluded that simulations to estimate a random expectation would be extraneous.

DISCUSSION

Contrary to our predictions, adult female cowbirds do not appear to facilitate dispersal of juvenile cowbirds from their hosts. Juvenile cowbirds typically were not located within their mother's home range when departing the forest and likewise, we detected only one brief (~30 min) juvenile departure event that temporally overlapped with the departure of the genetically assigned mother. As observed in some cowbird populations (e.g. Hahn & Fleischer, 1995; Hauber, 2002; Hauber et al., 2001), female cowbirds in this study were found inhabiting the forest during the postfledging period of juvenile cowbirds, thus providing the opportunity for juveniles to follow female cowbirds out of the natal habitat to social foraging flocks. Critically, we found no statistical differences in the dispersal behaviour of natal and transplanted juvenile cowbirds, or in the behaviour of local adult female cowbirds towards them, implying a lack of direct kin recognition in parasitic cowbird mothers. The ARTS detection analyses identified only four (out of 58 total) temporally correlated departures among juveniles and any radiotagged adult female. Although an unknown proportion of adult females inhabiting the forest were not radiotagged, the ARTS system monitored the occupancy of 11 females, and 60% of radiotagged juveniles were genetically assigned to a radiotagged female cowbird, indicating that a substantial proportion of females inhabiting the forest were radiotagged. In some instances, juvenile cowbirds may have followed females without radiotags, but we think that this is an unlikely explanation for the lack of juvenile departures coinciding with female cowbirds observed in this study.

For example, we detected multiple departure events from the forest for most juvenile cowbirds, increasing in probability and duration with age. In particular, we found that the greatest probability for juvenile departure was near sunset (1830–2130 hours), when adult female cowbirds (whether radioed or not) were unlikely to occur within the forest. Visual observations of juvenile cowbirds departing the forest and subsequently roosting solitarily within grasslands provided support for the departure pattern identified by the ARTS data.

Postfledging excursions at sunset and subsequent roosting may initiate independence from the host, thereby minimizing the possibility of sexually imprinting on the host species' phenotype. Solitary roosting has been demonstrated to increase with postfledging age in a few nonparasitic species, such as the mourning dove, *Zenaida macroura* (Hitchcock & Mirarchi, 1984), and the eastern screech-owl, *Megascops asio* (Belthoff & Ritchison, 1990), suggesting its potential importance for achieving independence from parental care and initiating natal dispersal. Juvenile birds are not fed during the night, which decreases their reliance on the natal habitat and (foster)parents. Therefore, departing at sunset may represent an optimal time to initiate exploratory excursions. Our study suggests support for a little explored alternative to maternally mediated conspecific recognition mechanisms in brood parasites (Hahn & Fleischer, 1995; Hauber, 2002): namely, genetic predisposition for specific roosting habitats that could induce juvenile cowbirds to depart from the natal habitat, thus initiating the process of independence from the foster parents (as we discuss below).

In addition to promoting spatial segregation from the host, juvenile excursions outside of the forest at sunset may also provide opportunities to locate conspecifics. Experimental manipulations of captive cowbirds have demonstrated that the production and recognition of cowbird song, and the development of appropriate social behaviours, are considerably experience dependent (Freed-Brown & White, 2009; King & West, 1983; O'Loghlen & Rothstein, 2010; West & King, 1988). Thus, the rapid discovery and joining of conspecific foraging flocks is critical for appropriate development. Adult cowbirds routinely fly to communal roosts in groups during the evening (Thompson, 1994; M. I. M. Louder, personal observation), and juvenile cowbirds departing from the forest prior to sunset would have the opportunity to locate conspecifics and potentially accompany adult cowbirds to a communal roost. Within the breeding season, brood parasitic Viduidae (Payne, 2010) and *Molothrus* cowbirds (Ortega, 1998) routinely roost with conspecifics, potentially revealing the importance of communal roosting to the evolution of brood parasitism. Therefore, roosting communally may not only enable individuals to find suitable foraging locations (information centre hypothesis: Ward & Zahavi, 1973; Weatherhead, 1983), but may also enable juveniles to adopt the songs and behaviours of conspecifics. Although we were unable to hand-track any radiotagged juvenile cowbirds to communal roosts, numerous adult females were observed associating with juveniles (all without radiotags) at a communal roost during July 2014 (M. I. M. Louder, personal observation), indicating that departing at sunset may play a role in the juvenile cowbird's ability to locate conspecifics.

Postfledging birds typically disperse to specific habitat types, often dissimilar to breeding locations of the adults (Cox, Thompson, Cox, & Faaborg, 2014). Postfledging habitats therefore, could promote the prevalence of conspecific interactions if habitat selection is largely innate (e.g. Grosch, 2004; Partridge, 1974), and shared among juvenile cowbirds and adults. Upon interaction with conspecifics within this habitat (e.g. grass pasture), genetically guided preferences for conspecific vocalizations (i.e. 'passwords'; Hauber et al., 2001) and learned components such as self-referent phenotype matching (Hauber, Sherman, & Paprika, 2000) would facilitate

conspecific recognition and subsequently enable the acquisition of appropriate behaviours. Although juvenile cowbirds are unlikely to follow adult females to foraging areas (this study), related juvenile–adult pairings could occur at a non-negligible baseline rate in specific habitat configurations and at specific local densities of cowbirds, as found by Hahn and Fleischer (1995) in upstate New York's fragmented landscape. Under this scenario, when a juvenile cowbird disperses from its natal area (alone) and locates a conspecific foraging flock, the probability that the flock contains its genetic mother is related to the number of accessible foraging flocks, the distance to the foraging flock and the density of local cowbirds.

Spatial segregation from hosts may be an important process in the development of juvenile brood parasites and the origin of brood parasitism. As in most cross-fostering experiments (ten Cate & Vos, 1999), captive juvenile brood parasites will sexually imprint on their host's phenotype when the associations are extended beyond the typical timeframe observed in nature (Freeberg et al., 1995; Sorenson et al., 2010). The redhead, an interspecific parasitic duck, primarily migrates to different wintering habitats than its host, which may enable parasitic offspring to avoid imprinting or reverse preferences acquired from interactions with the host (Sorenson et al., 2010). In support of this hypothesis, the lack of sexual imprinting observed in nonparasitic, but experimentally cross-fostered, pied flycatchers, *Ficedula hypoleuca*, may reflect the flycatcher's migratory behaviour and resultant limitation of social interactions with experimental foster species (Slagsvold, Hansen, Johannessen, & Lifjeld, 2002). While segregation behaviours of juvenile brood parasites may reduce the likelihood of misimprinting on their host's phenotype, it does not explain how juvenile brood parasites locate and recognize conspecifics. Genetic predispositions for habitat and phenotypic characteristics shared among conspecifics, in combination with cues learned from social interactions and self-inspection, are all likely involved in an obligate parasite's species recognition ontogeny (Göth & Hauber, 2004; this study). Furthermore, selection has probably favoured other mechanisms, such as delayed onsets or password-triggered flexibility in the sensitive periods of brood parasite offspring and future research investigating these factors will help increase our understanding of the origins and evolution of brood parasitism and its complex impact on social recognition and ontogeny.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2015.09.009.

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