Not just passengers: pigeons, *Columbia livia*, can learn homing routes while flying with a more experienced conspecific

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For animals that travel in groups, the directional choices of conspecifics are potentially a rich source of information for spatial learning. In this study, we investigate how the opportunity to follow a locally experienced demonstrator affects route learning by pigeons over repeated homing flights. This test of social influences on navigation takes advantage of the individually distinctive routes that pigeons establish when trained alone. We found that pigeons learn routes just as effectively while flying with a partner as control pigeons do while flying alone. However, rather than learning the exact route of the demonstrator, the paired routes shifted over repeated flights, which suggests that the birds with less local experience also took an active role in the navigational task. The efficiency of the original routes was a key factor in how far they shifted, with less efficient routes undergoing the greatest changes. In this context, inefficient routes are unlikely to be maintained through repeated rounds of social transmission, and instead more efficient routes are achieved because of the interaction between social learning and information pooling.

1. Introduction

When a group of animals travel together, its collective choice of route will affect what cues are available for spatial learning. Such group decisions can combine information from many group members (information pooling) or result from the group following certain individuals [1–3]. Several theoretical and empirical studies have demonstrated that individuals with more information will spontaneously emerge as leaders [2,4]. If the followers are simultaneously learning routes, it raises the possibility of these routes being perpetuated through social transmission [5]. Alternatively, followers may scrounge information without learning the routes themselves [6]. In addition, if several group members have their own information, learning during information pooling is likely to result in convergence on a more efficient route [7,8]. These various outcomes illustrate the potentially complex interactions between social learning and group decision-making in the context of collective animal navigation.

Social learning of migration routes is potentially widespread among bird species that migrate in multi-age flocks, and it could explain why long-distance migrants tend to form larger flocks [9]. There is evidence that migration routes are socially transmitted in storks, geese and cranes [10,11]. The most probable mechanism is local enhancement [12], whereby attraction to conspecifics brings an animal into contact with particular stimuli that it learns to use for its own orientation. Laboratory experiments have demonstrated that foraging routes can be socially transmitted in fishes [5,13,14]. In these studies, populations maintain particular routes even after the trained individuals (demonstrators) have been removed.
However, following a conspecific to a reward does not always result in effective learning. If the demonstrator is a reliable indicator of the reward, following can overshadow learning the task itself. Because of this overshadowing effect, the opportunity to scrounge food uncovered by a demonstrator can inhibit social learning [15,16]. In a spatial context, this is known as the ‘passenger/driver effect’. Burt de Perera & Guilford [6] found that accurate demonstration of the location of a food reward interferes with spatial learning by pigeons in the laboratory. However, there are numerous counter-examples from a range of species that learn from conspecifics despite scrounging [17–19], making it difficult to generalize the contexts and conditions where social learning will occur.

Furthermore, it is not clear how these mechanisms facilitating and inhibiting social learning affect spatial learning in a field setting, where the route choices of demonstrators are not physically constrained. Subjects in field experiments can discover new routes to rewards that were not part of the demonstrator’s pre-trained repertoire [19,20]. Although it is difficult to conduct controlled experiments on natural migration, two studies suggest that routes can be socially transmitted in the wild. One is an experiment on the daily routes taken by reef fish [21]. French grunts transplanted to new sites rapidly learned the routes of the resident fish schools, but only if the transplanted fish were allowed to interact with the residents. In another field experiment, cross-fostered white storks in their first year followed the migration direction of their foster population, as long as they departed the breeding area at the same time [10]. Although this demonstrates a social influence on migration direction, the sparse data from sightings and ringing recoveries do not indicate how much spatial detail of the migration route was socially transmitted. It is also not known how well the fostered storks learned the migration direction, as data on migrations in subsequent years are lacking.

Homing pigeons, *Columba livia*, offer the opportunity to study social learning of travel routes in a field setting. They naturally fly in flocks, they cope well with handling, and they can be made to fly home from the same location repeatedly over a short period of time, in contrast to wild bird migration. During the past decade, several studies using GPS loggers have revealed that over repeated homing flights from the same site, pigeons develop individually distinctive routes, which are most probably based on visual landmarks [22]. Furthermore, a pigeon with relatively little local experience can reach home by following a pigeon with an established route [4]. Here, we make use of this robust route-recapitulation phenomenon to examine the transmission of route information in a classic observer–demonstrator paradigm. We test whether repeated flights with a more experienced pigeon (one that has been allowed to build up greater local familiarity with a route over 18 consecutive pre-training flights) affect route learning in a less experienced partner, both in terms of the ability to learn a route and the location of the route learned.

In a previous study of social transmission during pigeon homing, Banks & Guilford [23] released pairs of pigeons in which one or both birds were naive to the release site. Naive pigeons with experienced partners reached home faster than those with naive partners, but the improvement was not maintained when the pigeons were subsequently released singly. This scrounging-induced overshadowing—a large-scale version of Burt de Perera & Guilford’s [6] passenger/driver effect—supports the conclusion that following a conspecific does not always result in learning. However, single-flight interactions are not ideal for studying the transmission of information because pairs often split up if one or both pigeons had never been released from that particular site before [23,24]. Our experiment improves on the design of Banks & Guilford [23] by releasing each observer–demonstrator pair multiple times, thereby providing the observer with additional opportunities to learn from their knowledgeable partner’s performance.

Our study investigates two questions about social learning in the context of pigeon homing. First, we test whether the observers learn a route while following a locally experienced demonstrator over repeated homing flights. We compare the solo performance of observers, which were each released with a demonstrator throughout their training, to controls, which were given the same number of training flights but alone. Since we know that route efficiency and fidelity reliably increase with the number of solo flights from a particular site [22], if following a demonstrator impairs spatial learning owing to overshadowing, we expect observers tested alone to take less efficient routes than controls and to recapitulate routes less closely. The second question, made possible by GPS tracking, is whether the solo routes of observers are more similar to those of their own demonstrators than other demonstrators. This will indicate whether the partner-following and route-learning processes have high enough spatial fidelity—and interact sufficiently—to maintain routes through social transmission.

2. Methods

(a) Subjects and experimental procedure

We used 44 homing pigeons between 2 and 7 years of age and of both sexes, housed at the Oxford University Field Station, Wytham, UK. They had been bred at Wytham or transferred from local breeders during their first year. Most had been involved in experiments in previous years, involving up to 50 homing flights (mean 18.3) from up to three different sites within 11 km of the loft. In the 2 months before the experiment, all subjects received basic training, which consisted of at least one flock release and three solo releases from four locations 2–3 km from the loft, in approximately the four cardinal directions. We alternated locations to minimize learned directional bias.

We replicated the sequence of experimental releases at two sites: site 1 was near South Leigh (home direction 74.0°, distance 7.05 km), and site 2 was near Elsfield, a similar distance from the loft in the opposite direction (home direction 291.1°, distance 7.73 km). The two release sites were at least 3 km away from any sites where these pigeons had been released in previous experiments. We randomly allocated subjects into four groups of 10: demonstrators, observers, site 1 controls and site 2 controls. At site 2, we re-used the demonstrators and observers from site 1 with their roles reversed, so that demonstrators from site 1 became observers at site 2 and vice versa. We kept the same demonstrator–observer pairings at both sites, so that the randomly occurring differences in experience, age and sex at site 1 were exactly reversed at site 2. This provided a more systematic way to control these factors than if we had randomly re-paired the demonstrators and observers. Four additional subjects were added to the site 2 groups to replace demonstrators or observers who failed to return during training from site 1, or whose Velcro strip (see below) became too loose to attach a GPS tracker. In
total, seven demonstrator–observer pairs and 10 controls com-
pleted the experiment at site 1, plus 10 demonstrator–observer
pairs and nine controls at site 2.

We completed the full sequence of experimental releases at
site 1 before switching to site 2. The sequence at each site
lasted 4 to 5 weeks, with up to four releases per bird per day
and a minimum of 1 h rest period between releases. Pigeons
were transported to the release sites in aluminium boxes inside
a car with the windows open to allow access to atmospheric
odours. Transportation time was approximately 20 min to site 1
and 17 min to site 2. We released birds during daylight hours
in dry weather with wind less than 7 m s⁻¹.

The sequence of releases at each site consisted of three
phases: demonstrator pre-training, paired/control training and
solo tests. Demonstrator pre-training (administered only to
birds designated as demonstrators) consisted of 18 solo flights
to allow each demonstrator to establish an idiosyncratic homing
route and to create an asymmetry in local homing experience
between demonstrators and observers. For the paired/control
phase, we randomly paired each demonstrator with an observer,
and released each pair 12 times. In parallel, control subjects received the same number of training flights as
observers, but alone rather than in pairs. The release order
each day alternated between controls and pairs, so that the treat-
ment groups experienced the same weather conditions, time of
day and trial spacing. We chose 12 releases for the paired/control
training phase, as this number of releases allowed controls to
begin to develop landmark-based routes, while also allowing us
to move past the initial phase of paired training during which
observer pigeons frequently split from their demonstrators.
Finally, the solo tests consisted of releasing every bird singly
three times to test route memory retention and solo homing per-
formance. At both sites, solo flights began the day immediately
after paired training, using a randomization test. We also
aimed to test whether route similarity within these real pairings
(i.e. whether the routes observed were more similar than those
we would have expected at random). There were 17 pairs
of routes in each test: seven from site 1 and 10 from site 2. We
quantified within-pair similarity using the median inter-route
distance (M_do). Then we randomly re-paired the routes, with
the restriction that pairings had to be between routes from the
same site. We calculated the median inter-route distance for
each randomization (M_r), and used 10 000 randomized pairings
to build up a test distribution of this statistic. For a two-tailed sig-
nificance test, the p-value was the proportion of M_r values that
fell farther from the mean than M_do.

To compare route learning of observers and controls, we cal-
culated two metrics describing their homing routes during the
solo test phase. First, we quantified homing route efficiency
using distance from beeline, i.e. the distance from each point
on the bird’s GPS track to the nearest point on a straight-line
path composed of 1000 points, averaged for all points on the
track. Second, we quantified route fidelity as the mean variance
between each bird’s three solo test tracks. To find the mean var-
iance, we calculated the variance at each point along the mean
route using the distances to the nearest points on the three GPS
tracks, and then averaged the variances from the 500 points com-
prising the mean route [25]. We normalized both metrics using a
log-transformation, and compared the observer and control treat-
ments using a two-way ANOVA that also took into account any
effect of release site (R v. 3.1-102, [26]). We used the same test to
analyse the effect of treatment on distance to beeline at the begin-
ning and end of the paired training phase. We also calculated the
distance from beeline and the variance of the original demonstra-
tor routes (mean of tracks 16–18), and then tested the effects of
these route properties on how well the routes were subsequently
transmitted to observers, again using a linear model in R that
took into account any effect of release site.

3. Results

(a) Demonstrator pre-training

Homing efficiency of demonstrators improved significantly
over the course of the pre-training flights, with a 16–80% decrease in path length between the first and eighteenth flight
(mean 58.9%, see the electronic supplementary
material, figure S1). Distance to the beeline decreased in all
but one of the demonstrators (mean decrease of 1230 m, Wil-
coxon signed-rank test p < 0.001). At the end of pre-training,
demonstrators were also significantly closer to the beeline
than were the controls on their first solo flight (two-
way ANOVA, F_1,33 = 25.8, p < 0.001 for treatment effect,
F_1,33 = 0.98, p = 0.330 for site effect; figure 2a). Therefore, it
is meaningful to refer to the demonstrators as having greater
local familiarity than observers and controls at this stage in

(b) Data logging and analysis

We tracked all flights using 1 Hz micro-GPS data loggers (iGotU,
Mobile Action Technology). The loggers weighed 20 g and were
attached to pigeons via a strip of Velcro glued to trimmed feathers
on the back. When the pigeons returned to the loft, we
removed the loggers and downloaded the data to a computer using
FUGAWI software (Mobile Action Technology). We ana-
lysed tracks in MATLAB (MathWorks, release 2010b). We
converted positional data from degrees to metres using a Uni-
versal Transverse Mercator grid. In order to focus on the choice
of homing route, we only used the segment of track from when a
pigeon first passed outside a 200 m radius of the release site to
when it first entered a 200 m radius of the loft, thereby excluding
birds’ initial circling of the release site immediately after take-off
and their circling of the loft immediately prior to landing. We super-
imposed tracks onto Ordnance Survey maps using FUGAWI software
(Northport Systems Inc.). The GPS track data are available through
the Dryad repository (doi:10.5061/dryad.5344b).

To reduce the number of comparisons between tracks, we
first calculated mean routes from each set of a pigeon’s three consecutive GPS tracks, using the method of Freeman
et al. [25]. Over 100 iterations, this method finds a mean path
of 500 points that minimizes the distance to nearest neighbouring
points on the original GPS tracks, while ensuring that the dis-
tance between consecutive points on the mean path is more
than 5 m. There were two mean routes which we calculated
using only two GPS tracks because the third track was lost
owing to GPS device failure.

We tested whether observers’ routes from the solo test were
significantly similar to their demonstrators’ routes immediately
before paired training, using a randomization test. We also
used a randomization test to check for within-individual consist-
ency among demonstrators, by comparing their ultimate and
penultimate mean routes from pre-training. With additional ran-
domization tests, we compared observer routes during paired
training to demonstrator routes immediately before paired train-
ing, to test whether observers had been following demonstrators.
In all cases, we quantified the similarity between two mean
routes by finding the distance from each point on one route to
the nearest neighbouring point on the other, applied reciprocally
and averaged over the length of the routes.

Each randomization test compared real pairings with ran-
domized pairings. Real pairings were either two routes from the
same bird or one each from an observer–demonstrator pair. We
aimed to test whether route similarity within these real pairings
was significantly higher than in randomized pairings
(i.e. whether the routes observed were more similar than those
we would have expected at random). There were 17 pairs
of routes in each test: seven from site 1 and 10 from site 2. We
quantified within-pair similarity using the median inter-route
distance (M_do). Then we randomly re-paired the routes, with
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the experiment, especially given that repeated solo training improved homing efficiency.

After 18 solo pre-training flights, demonstrators were stably recapitulating homing routes (red routes in figure 1 and electronic supplementary material, figure S1). To test whether the demonstrator routes were individually distinctive, we compared the mean route from pre-training flights 13–15 to the mean route from flights 16–18. Distance between these consecutive mean routes was 107 ± 80 m at site 1 and 276 ± 362 m at site 2, whereas the distance between the routes of different demonstrators in pre-training flights 16–18 was 553 ± 411 m at site 1 and 654 ± 547 m at site 2. A randomization test confirmed that demonstrators flew closer to their own previous route than to the previous route of a randomly selected demonstrator (p = 0.040).

(b) Paired releases

Each demonstrator–observer pair was released 12 times, and they homed together on a mean of 8.65 ± 1.87 releases. We classified a pair as having split if they became separated by more than 150 m at any point on the homeward flight. During the first paired release, all but one of the 17 observers split from their demonstrators, but over the course of the remaining paired releases the observer–demonstrator pairs split less often. If splitting was due to unfamiliarity with the partner or with the experimental procedure, rather than unfamiliarity with the site, one would expect less splitting at site 2 than at site 1. However, splitting did not vary significantly between the sites (mean flights with split: 3 ± 1.8 at site 1, 3.8 ± 2.7 at site 2, Wilcoxon rank sum test p = 0.58). The mean observer routes from paired flights 4–6, 7–9 and 10–12 were all significantly similar to their demonstrators’ pre-training routes (randomization tests: p = 0.022, p = 0.003, p = 0.044), indicating that observers were generally following demonstrators close to the pre-trained routes.

However, not all demonstrators maintained their pre-trained routes when flying with observers. On the whole, demonstrators’ homing routes shifted significantly closer to the beeline, away from their previously established routes (figure 2). While most demonstrator routes shifted by less than 200 m, a few demonstrators at each site adopted completely new homing routes that were much more direct than before paired training (figure 2c). Demonstrator routes that were initially farther from the beeline shifted more during the paired training phase (F1,14 = 28.21, p < 0.001, from a linear model with release site as a fixed factor). The indirect demonstrator routes in figure 1e,f are among those that subsequently shifted by large amounts during paired training.

(c) Route learning by observers

To assess the impact of paired training on observers, we compared the homing routes of observers and controls. Control
pigeons showed a significant improvement in homing efficiency over their first 12 solo flights. Eighteen out of 19 reduced both their path length (mean reduction of 68.4%, Wilcoxon sign rank \( p < 0.001 \)) and their mean distance to the beeline (mean reduction of 5527 m, Wilcoxon sign rank \( p < 0.001 \); electronic supplementary material, figure S1).

The observers, each released with a demonstrator, were initially closer to the beeline than controls (figure 2a; two-way ANOVA comparing observer and control distance to beeline in flights 1–3, \( F_{1,33} = 18.40, \ p < 0.001 \) for treatment effect, \( F_{1,33} = 4.75, \ p = 0.036 \) for site effect). However, by the end of the training, the average distance from the beeline did not depend on whether the pigeons flew singly or in pairs (flights 10–12: \( F_{1,33} = 0.58, \ p = 0.453 \) for treatment effect, \( F_{1,33} = 10.89, \ p = 0.002 \) for site effect).

Afterwards, when the observers flew alone in the solo tests, their distance from the beeline was not significantly different from that of controls (figure 3a; \( F_{1,33} = 0.31, \ p = 0.581 \) for treatment effect, \( F_{1,33} = 9.99, \ p = 0.003 \) for site effect). In addition, there was no significant difference between observers and controls in their degree of route recapitulation during solo tests, measured as the mean spatial variance of the three homing routes about their mean route (figure 3b; \( F_{1,33} = 1.22, \ p = 0.277 \) for treatment effect, \( F_{1,33} = 5.34, \ p = 0.027 \) for site effect). This indicates that paired training over 12 consecutive releases did not affect route learning compared with what birds achieve individually, at least in terms of the directness and fidelity of routes. Homing routes from site 1 tended to be more direct and more accurately recapitulated than those from site 2. The effect of site did not depend on treatment (interaction terms added to above ANOVA models: \( F_{1,33} = 0.41, \ p = 0.527 \) in distance-from-beeline model; \( F_{1,33} = 0.97, \ p = 0.333 \) in route-variance model).

(d) Transmission of route information
The mean distance from observer solo routes to their demonstrators’ pre-paired route was 312 ± 262 m at site 1 and 370 ± 553 m at site 2. Large standard deviations and positive skew at both sites indicate that a minority of
observers learned very different routes from their demonstra-
tors. The observer routes that closely match the original
routes of their demonstrators tend to be near the beeline
(figure 1a–d), where it is difficult to detect information trans-
mission because of the low diversity among demonstrator
routes, and where the routes are likely to be similar even if
they were learned independently. Separate randomization
tests for each site found significant demonstrator–observer
route similarity at site 2 \( (p = 0.014) \) but not at site 1
\( (p = 0.330) \), indicating that there was some transmission of
route information but that the effect was not consistent.
A combined randomization test showed that overall the
observer routes were not significantly closer to their own
demonstrators’ routes than to randomly chosen demonstrator
routes from the same release site \( (p = 0.250) \).

We used a linear mixed-effects model to test which
features of the pre-training and post-training routes pre-
dicted high observer–demonstrator route similarity. Given
that indirect demonstrator routes shifted farther during
paired training, it is not surprising that the farther from the
beeline the original demonstrator route, the less similar
it was to the final observer route \( (F_{1,12} = 43.71, p < 0.001) \). There was no significant effect
from the demonstrator’s route variance during pre-training
\( (F_{1,12} = 2.02, p = 0.181) \) or the number of flights on which
the pair split \( (F_{1,12} = 0.56, p = 0.468) \).

4. Discussion
Our study used GPS tracking to examine how flying with a
more locally experienced partner affects both a pigeon’s
ability to learn a homing route and the shape of the route
it learns. Following a conspecific did not overshadow
route learning, but neither did it facilitate learning—obser-
vaters learned routes that were just as efficient and just as
accurately recapitulated as those of controls flying alone.
Given that observers did learn routes, one might expect
their routes to be similar to the initial routes of their respect-
ive demonstrators. However, there was no consistent pattern
of social transmission (figure 1), largely because demonstra-
tors shifted their routes over the course of repeated flights
with observers. This suggests that observers were not only
able to learn landmark-based routes, but also that they
may have taken an increasingly active role in the pair’s
navigation as a result of learning.

Our finding that observers learned just as well as controls
contrasts with previous laboratory-based studies of pigeons, in
which the opportunity to scrounge a food reward from a knowl-
edgeable conspecific inhibited the learning of a food-extraction
technique [15] or food location [6]. There are several factors
that could account for the difference in results. In Burt de
Perera & Guilford’s study [6], the small spatial scale meant
that the demonstrator and the reinforcer (food) were closely
paired in time and space compared with our study. Another—
probably very important—difference was the use of repeated
training, which gave observers in our study additional opportu-
nities and time to learn routes. Our results do not rule out an
overshadowing or passenger/driver effect in the earlier stages
of route learning, as found by Banks & Guilford [23]. Their
study also used a more difficult navigational task than ours,
with the longer homing distance and lower experience of sub-
jects at the start of the experiment perhaps contributing to the
overshadowing effect they found.

The development of homing routes over repeated solo
releases by our demonstrator pigeons was fully expected given
previous studies [22,27]. Despite the relatively short homing dis-
tance and the subjects’ previous experience, we were able to use
this route-learning phenomenon to create a significant asymme-
try in local route familiarity between demonstrators, with
established routes, and observers or controls. Routes from
the solo test phase were straighter and more accurately recapitu-
lated at site 1 than at site 2. This site effect was equally strong in
observers and controls, even though controls had experience
with only one site. While it is possible that the observers at
site 2 had difficulty learning new routes because of their prior
experience at site 1, a more likely explanation is that geogra-
phical factors underpin these differences in flight paths. The
greater difficulty of the homing task from site 2 may explain
why we detected social transmission at site 2 but not site 1:
i) a more difficult homing task increases the likelihood that
observers will use social information [4], and (ii) higher diver-
sity among demonstrator routes makes social learning easier
to detect. An alternative explanation is that the observer–
demonstrator pairs were already familiar with each other,
and with the experimental procedure, from their use at site 1.
However, if familiarity with the partner facilitated social infor-
mation use, we might expect pairs to split less often at site 2,
which was not the case.

The shift in demonstrator routes during the paired train-
ing phase was unexpected, and it interfered with the
accurate social transmission of routes to observers. Although
some of the shift can be attributed to gradual improvement
with additional homing experience, in some cases demonstra-
tors shifted their routes by hundreds of metres. This
behaviour is surprising because it breaks with the asymptotic
increase in efficiency normally seen over repeated homing
flights, during which pigeons flying alone continue to recapitu-
late relatively indirect routes even after as many as 24 releases [22].
A future study could test whether flying
with the observers was responsible for the improvement in
our demonstrators’ routes, using an additional control

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