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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 259.1°, 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 completed 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 treatment 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 performance. At both sites, solo flights began the day immediately following the final paired flight and were completed within 2–4 days, depending upon weather conditions.

(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 the iFIND PC software (Mobile Action Technology). We analysed tracks in MATLAB (MathWorks, release 2010b). We converted positional data from degrees to metres using a Universal 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 superimposed tracks onto Ordnance Survey maps using the FUGAWI software (Northport Systems Inc.). The GPS track data are available through the Dryad repository (doi:10.5061/dryad.534tb).

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 distance between consecutive points on the mean path is more than 5 m. There were two mean routes which we calculated 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 variance, 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 comprising the mean route [25]. We normalized both metrics using a log-transformation, and compared the observer and control treatments 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 beginning and end of the paired training phase. We also calculated the distance from beeline and the variance of the original demonstrator 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, Wilcoxon 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
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 \( (F_{1,14} = 28.21, p < 0.001, \text{ from a linear model with release site as a fixed factor}) \). The indirect demonstrator routes in figure 1c,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.
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).

Figure 2. Development of homing routes in demonstrator (red lines) and observer (blue lines) birds (green line denotes controls). (a) Mean distance from homing routes to the beeline, by treatment group, pooled across both sites. Bars show s.e.m. (b) Distance to the final solo demonstrator track recorded immediately before paired training. (c) Histogram showing shift in demonstrator routes during paired training (mean distance during solo test—mean distance during paired flights 10–12). Median is significantly below zero, indicating routes got closer to beeline (Wilcoxon signed-rank test, $p = 0.006$, $n = 17$).

(d) Transmission of route information

The mean distance from observer solo routes to their demonstrators’ pre-paired route was $312 \pm 262$ m at site 1 and $370 \pm 553$ 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-
mision 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 (figure 4; linear model,
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-
vers 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 recapiti-
tuate 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
group that flew home singly the same number of times as
demonstrators. If adding observers leads to straighter
routes, then repeated rounds of learning will converge on a
more efficient solution rather than faithfully perpetuating inefficiences, similar to the ‘hill climbing’ property of social
learning in nine-spined sticklebacks [28]. This does not
require any sophisticated selective copying strategy, but
could emerge from the interaction between learning and fol-
lowing in both demonstrators and observers.

If the paired routes combined information from both birds,
then the pairs’ increase in homing efficiency is less surprising
[8,29]. Although observers were not as proficient as demonstra-
tors at the start of paired training, they did have their own
navigational information from sources such as olfaction, a
sun compass and geomagnetism [30,31], as well as landmarks
seen, perhaps less locally, during previous experiments and
during early flights when they split from their demonstrators.
With this information, the observer may be able to influence
the trajectory of the pair and therefore shape the content of
the local enhancement process, rather than just follow passively.
The observer’s probability of leading would have increased as it
gained more local experience over repeated homing flights [4].
Where alternative routes to a reward are easy for individuals
to discover on their own, arbitrary traditions are not likely to
be maintained, as Thornton & Malapert [20] found in meerkats.
In guppies, social transmission of a circuitous route to food is
less persistent than social transmission of a short route [5].
These studies, along with ours, demonstrate that animals can
avoid social learning’s potential cost in perpetuating relatively
inefficient behaviour.

This is, to our knowledge, the first field experiment on
birds to investigate whether the distinctive shape of a route
can be transmitted from one individual to another, a type of
social learning that is potentially widespread among species
that migrate or forage in groups. For pigeons, following a
more experienced individual and learning a landmark-based
route are not mutually exclusive strategies, but can happen
in parallel. However, rather than resulting in the accurate
social transmission of homing routes, the demonstrators’ orig-
inal routes shifted over repeated interactions, possibly owing
to input from the less locally experienced pigeon. Our results
support an interaction between information pooling and
social learning. Although learning-while-following offers a
mechanism for the maintenance of socially transmitted
migratory routes, such a tradition will not persist if newcomers
have inherent navigational abilities that allow them to
discover new routes and influence the path of the flock.

The protocols outlined in this paper were approved by the Ethical
Review Committee of Oxford University’s Department of Zoology.
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