Integrating animal movement with habitat suitability for estimating dynamic landscape connectivity

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Date of the manuscript draft: March 24, 2017

Manuscript word count: 8427

Abstract

Context High-resolution animal movement data are becoming increasingly available, yet having a multitude of trajectories alone does not allow us to easily predict animal movement. To answer ecological and evolutionary questions at a population level, quantitative estimates of a species' potential to act as a link between patches, populations, or ecosystems are of importance.

Objectives We introduce an approach that combines movement-informed simulated trajectories with an environment-informed estimate of their ecological likelihood. With this approach, we estimated connectivity at the landscape level throughout the annual cycle of bar-headed geese (*Anser indicus*) in its native range.

Methods We used a tracking dataset of bar-headed geese to parameterise a multi-state movement model and to estimate temporally explicit habitat suitability within the species' range. We simulated migratory movements between range fragments, and estimated their ecological likelihood. The results are compared to expectations derived from published literature.

Results Simulated migrations matched empirical trajectories in key characteristics such as stopover duration. The estimated likelihood of simulated migrations was similar to that of empirical trajectories. We found that the predicted connectivity was higher within the breeding than in wintering areas, corresponding to previous findings for this species.

Conclusions We show how empirical tracking data and environmental information can be fused to make meaningful predictions about future animal movements. These are temporally explicit and transferable even outside the spatial range of the available data. Our integrative framework will prove useful for modelling ecological processes facilitated by animal movement, such as seed dispersal or disease ecology.

Keywords

Anser indicus, bar-headed goose, empirical random trajectory generator, migration network, movement model, null model for migration, simulation

Introduction

The observation and banding of individuals, and more recently remote tracking, have provided insights into how, when, and where animals move (Hussey, Kessel, *et al.*, 2015; Kays, Crofoot, *et al.*, 2015). The miniaturisation of tracking technologies permits scientists to follow ever more individuals of ever smaller species, providing a more detailed picture of individual behaviour. Remote tracking data are an especially rich source of information for the understanding of movement behaviour and its wider ecological implications (e.g., Mueller, Lenz, *et al.*, 2014), such as the linking of patches, populations, or ecosystems by offering dispersal opportunities for seeds, propagules, and pathogens (Bauer and Hoye, 2014).

Currently, there is an increasing availability of tracking technologies, allowing us to gather highly detailed information about the movement and physiology of tracked individuals. However, the number of individuals that scientists are realistically able to track will remain minuscule compared to even the most conservative estimates of the numbers of migrating individuals. The estimation of population-level movement patterns is, however, pivotal to the understanding of how animals function as links in space, and thus fundamental to answering central ecological and evolutionary questions. This leads to an increasing need to derive informed estimates about the behaviour of populations from few, well-studied individuals. However, such generalisations are not straightforward, mainly because the movement behaviour of individuals and the observed variation may not be representative for the population or the whole species (e.g., Austin, Bowen, *et al.*, 2004). The movement behaviour of individuals is thus not only influenced by general species properties, but also individual variation and the surrounding environmental conditions (Nathan, Getz, *et al.*, 2008). Any kind of movement behaviour is thus to some extent unique to the individual, explicit in time, space, and the environmental conditions as well as specific in the ecological consequences that arise from it. We argue that the combination of movement trajectories with remotely sensed environmental information can nonetheless be used to predict animal movement and landscape connectivity.

Most methods that have been developed to derive predictions of animal movement, however, are either based purely on the actual movement process (movement-informed) or use environmental correlates to predict the likelihood of animal movement in space (environment-informed). Examples for movement-informed processes are dispersal kernels (e.g., Jordano, García, *et al.*, 2007) which represent a probability distribution determined by the distance

travelled over time, or movement models such as correlated random walks (CRW, Codling, Plank, *et al.*, 2008) that are informed by distributions of step length and turning angle. Both are used to predict the movement of an individual from a given starting point, but often remain ignorant to the surrounding environment. Environment-informed processes, in contrast, use environmental correlates to predict the likelihood of animal movement in a certain landscape, which is often achieved using cost- or resistance-based approaches (e.g. CircuitScape, McRae, Dickson, *et al.*, 2008, and least-cost paths, Ferreras, 2001; Graham, 2001). These methods predict the most likely path between defined start- and endpoints given a certain assumption about the kind of environments an animal is likely to move through (LaPoint, Gallery, *et al.*, 2013). However, in contrast to movement-informed approaches, these most likely paths do not necessarily have inherent temporal explicitness nor do they adhere to the characteristics inherent to a species' movement. Thus, although the use of resistance surfaces can provide an impression of the paths connecting habitat patches in fragmented landscapes, we cannot derive direct estimates for the time that would be necessary to travel from start- to endpoint for the individual or any given species.

We suggest that the combination of movement-informed path modelling and environment-informed suitability models form the basis that define relevant null models for animal movement. As demonstrated by the application of step-selection functions (Fortin, Beyer, *et al.*, 2005; Thurfjell, Ciuti, *et al.*, 2014), an approach that accommodates both movement characteristics and the environment can yield functional estimates for animal movement across a landscape (e.g., Richard and Armstrong, 2010). Step-selection functions were specifically designed for the estimation of resource selection by animals moving through a landscape (Thurfjell, Ciuti, *et al.*, 2014), but can also be used to estimate connectivity between patches (Squires, DeCesare, *et al.*, 2013) or to simulate trajectories that are informed by the environmental conditions. However, step-selection functions are currently not capable of estimating connectivity between fixed starting and end locations, or of considering more than one behavioural mode (but see Thurfjell, Ciuti, *et al.*, 2014 for suggestions). To estimate how animals can act as links in space beyond the spatial range of observation it is pivotal to quantify connectivity between defined locations, e.g. patches or populations. Here, it is of crucial importance to maintain the geometry of a species' movement (as observed using a fixed sampling rate), which is amongst others determined by speed and turning angles, their covariance and their (auto)correlative structure.

In this study, we introduce a novel concept that can generalise from a limited set of trajectories to a species level connectivity landscape by combining movement-informed and environment-informed processes. This approach realistically accounts for the movement capacities of individuals while maintaining the ecological plausibility of simulated trajectories as determined by environmental correlates: a **M**ovement-informed and **E**nvironmentally-evaluated **L**andscape **C**onnectivity (**MELC**). We use movement models that are parametrised by empirical tracking data, and maintain the empirically derived geometric properties to simulate realistic trajectories between defined start- and endpoints. We retrospectively evaluate each of these trajectories using habitat suitability models to derive an **e**cological **li**kelihood of **R**andom **T**rajectories (**eliRT**). We exemplify the MELC concept by adapting the simulation of trajectories for a specific movement behaviour, the stepping-stone like migration of bar-headed geese (*Anser indicus*, Latham 1790), and estimate the mean likelihood of simulated trajectories connecting the patches within the species native range. Based on these random trajectories we derive a MELC network that quantifies the average likelihood of migration between range fragments based on the joint likelihood of movement properties and the ecological conditions (see also Figure 1). Finally, we demonstrate how seasonal changes influence this MELC network, and compare our results with the current knowledge.

Simulation and evaluation of trajectories

Both the simulated trajectory and the assessment of its ecological likelihood should reflect the movement ecology of the species in question. The movement model used for simulation should thus encompass all relevant naturally occurring modes of movement, and how the environment affects the individual's movement behaviour. The migration behaviour of bar-headed geese is typical for a species that primarily uses powered flight for locomotion: it is characterised by fast and directed non-stop movements interspersed with extended staging periods at suitable stopover sites (Hawkes, Balachandran, *et al.*, 2011). The availability of high-quality stopover sites en route is crucial to the migrating individuals, as they have to replenish their energy reserves during these staging periods (Drent, Eichhorn, *et al.*, 2007). On the other hand, bar-headed geese are capable of covering large distances quickly, and even the Himalayas pose no insuperable challenge to this species (Bishop, Spivey, *et al.*, 2015). For this reason, suitable stopover areas are likely the most critical resource during migration (see also Green, Alerstam, *et al.*, 2002), and their availability

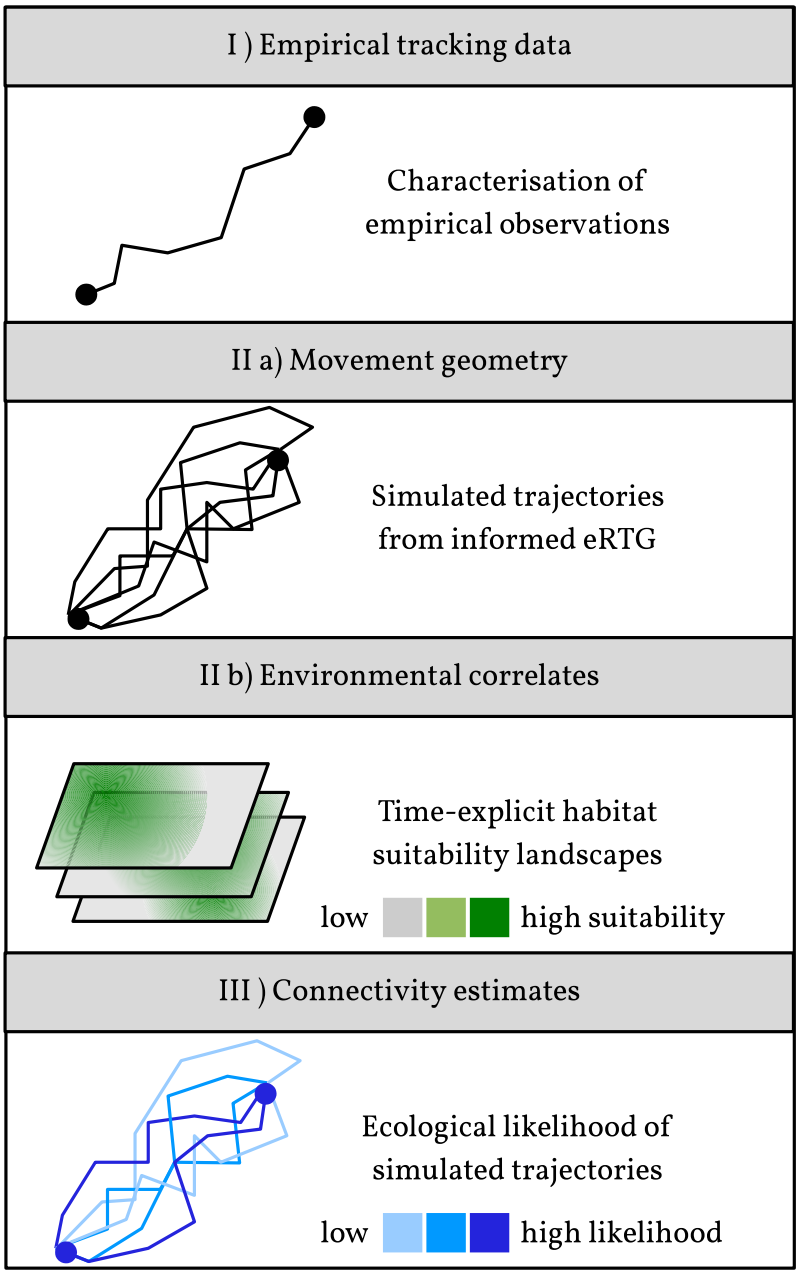

Figure 1. General concept of the movement-informed and environmentally-evaluated landscape connectivity (MELC): I) Empirical tracking data are IIa) used to derive an informed eRTG to simulate conditional movement between sites of interest, and IIb) combined with environmental correlates to derive predictions of relevant measurements of landscape permeability (here: suitability of stopover sites). III) Finally, the simulated conditional trajectories are evaluated based on characteristics of the trajectory and permeability using an informed measure of ecological likelihood.

should thus be decisive for the ecological likelihood of simulated trajectories.

For our approach, we used a recently developed movement model, the **e**mpirical **R**andom **T**rajectory **G**enerator (**eRTG**, Technitis, Weibel, *et al.*, 2016; Technitis, Weibel, *et al.*, in preparation), and extend it by incorporating a switch between the two main modes of bar-headed

goose migration, migratory flights ("*migratory behaviour*") and movements during stopover periods ("*stopover behaviour*"). We derived the necessary parameters for both movement modes, and the probability of transitioning between these modes, directly from the tracking data. Every trajectory simulated with the eRTG replicates the geometric properties of empirical tracks, and with our additions, the transitions between migratory flight and staging, and their respective durations. To estimate the suitability of simulated stopover sites, we derived habitat suitability models based on position information from the tracking data in combination with remotely sensed environmental information. As Zeigler and Fagan (2014) already pointed out, however, connectivity is not necessarily constant over time. Both the environment and the habitat requirements of a species are subject to seasonal changes, and consequentially, the ecological likelihood of simulated trajectories should fluctuate as well. A segmentation by habitat use (van Toor, Newman, *et al.*, 2016) allows us to detect periods of time for which the interactions between habitat use and habitat availability are consistent. This forms the basis for a time-explicit habitat suitability model on which the simulated trajectories can be evaluated explicitly in space and time. Our approach incoporates potential changes in habitat suitability into the assessment of the ecological likelihood of trajectories and thereby assesses the dynamics of the connectivity landscape over the annual cycle.

Just as the quality of available stopover sites is decisive of how well migratory individuals can replenish their reserves, so is the time they spend staging at those sites. In particular, during spring migration, the arrival at the breeding grounds needs to be well-timed with the phenology of their major food resources (Bauer, Gienapp, *et al.*, 2008). Too early an arrival can result in a food shortage, while latecomers might find all suitable nesting sites already occupied (Prop, Black, *et al.*, 2003; Bêty, Giroux, *et al.*, 2004; Brown and Brown, 2000; Madsen, Tamstorf, *et al.*, 2007). For this study, we make two main assumptions about the ecological likelihood of simulated migrations: (1), it is desirable to reach the destinations quickly, i.e. staying at a stopover site comes at the cost of delaying migration, and (2), if a stopover site is used, the cost of the delay is affected by its habitat suitability, i.e. the use of superior stopover sites can counterbalance the cost imposed by delaying migration. If we want to estimate the connectivity between two locations a and b, e.g. the nest site and the wintering location of an individual, we can simulate i migrations using the modified eRTG. Each trajectory j can be characterised by a total migration duration $t_{a,b,j}$ which consists of the total flight time $\tau_{a,b,j}$ and the total time spent at stopover sites $\Delta_{a,b,j}$.

The total stopover time $\Delta_{a,b,j}$ is the sum of the time spent at each visited stopover site and is thus $\Delta_{a,b,j} = \sum_{k=0}^{n} \delta_k$, where δ_k is the time spent at the k-th of $n \in 0, 1, ..., \mathbb{N}$ stopover sites. We define the relative delay $D_{a,b,j}$ caused by using stopover sites for trajectory j between a and b as

$$D_{a,b,j}(t,\tau) = \frac{\tau_{a,b,j}}{\tau_{a,b,j} + \Delta_{a,b,j}} = \frac{\tau_{a,b,j}}{t_{a,b,j}} \tag{1}$$

This delay $D_{a,b,j}$ is, however, mediated by the benefit b an individual gains at the stopover site, e.g. by replenishing its fat reserves. Here, we define that the benefit gained by staying at a stopover site k, b_k, is proportional to the time spent at site k, δ_k, and the habitat suitability of site k, S_k. We thus define the benefit of any stopover site k as

$$b_k(S,\delta) = S_k \times \delta_k \tag{2}$$

We assume the effects of several sequential stopovers to be cumulative, and thus define the total benefit of a migratory trajectory j between sites a and a with n stopovers as

$$B_{a,b,j} = \sum_{k=0}^{n} (S_k \times \delta_k) = \sum_{k=0}^{n} (b_k) \tag{3}$$

Finally, we define the ecological likelihood *eli* of any trajectory j as a function of both the delay caused by using stopovers and the cumulative benefit of these stopovers:

$$eli_{a,b,j} = \frac{\tau_{a,b,j}}{\tau_{a,b,j} + \Delta_{a,b,j} - B_{a,b,j}} = \frac{\tau_{a,b,j}}{t_{a,b,j} - B_{a,b,j}} \tag{4}$$

In this way, the ecological likelihood of a trajectory with no stopovers and a trajectory with stopovers of the highest possible quality will be equal, and is defined solely by the time the individual spent in migratory mode ($eli = 1$). For trajectories with stopovers in less than optimal sites, however, the likelihood is relative to both the staging duration and quality of stopover sites, and should take values of $\frac{1}{D_{a,b,j}} < eli_{a,b,j} < 1$. Using this metric, we assessed simulated trajectories in a way that is biologically meaningful for bar-headed geese and potentially other waterbird species with similar migratory strategies.

A MELC network for bar-headed geese

We modelled connectivity within the native range of bar-headed geese, a species that naturally occurs in Central Asia ($68-107°N$, $9-52°E$). According to BirdLife International and NatureServe (2013), both the breeding and wintering range are separated into four distinct range fragments (see also Figure S1), with minimum distances between range fragments ranging from $79km$ to $2884km$. For our application of the MELC, we investigated how well these range fragments can be connected by simulated migrations of bar-headed geese.

The migratory routes for some populations of bar-headed geese are known (e.g., Hawkes, Balachandran, *et al.*, 2011; Guo-Gang, Dong-Ping, *et al.*, 2011; Prosser, Cui, *et al.*, 2011; Bishop, Yanling, *et al.*, 1997; Takekawa, Heath, *et al.*, 2009). These tracking studies have revealed that large parts of the respective populations migrate from their breeding grounds in Mongolia, northern China and on the Tibetan Plateau over the Himalayas to their wintering grounds on the Indian subcontinent. But while the crossing of the Himalayas has been studied in great detail (Hawkes, Balachandran, *et al.*, 2011; Hawkes, Balachandran, *et al.*, 2013; Bishop, Spivey, *et al.*, 2015), less is known about the connectivity between range fragments both within the wintering and within the breeding range (Takekawa, Heath, *et al.*, 2009). Stable isotope analyses suggested that the connectivity within the breeding range of bar-headed geese is relatively high (Bridge, Kelly, *et al.*, 2015), a notion that has been supported by tracking data as well (Cui, Hou, *et al.*, 2010). In the wintering range, however, relatively few movements have been observed (Kalra, Kumar, *et al.*, 2011).

In this study, we used the range data available from BirdLife International and NatureServe (2013) to simulate migrations of bar-headed geese between the fragments of the species' range. We associated all simulated trajectories with the corresponding ecological likelihoods and compared them to empirical trajectories. By averaging over populations of trajectories, we generalised and derived a network that predicts migratory connectivity between the fragments of the species range. Based on the findings of previous studies (Bridge, Kelly, *et al.*, 2015; Kalra, Kumar, *et al.*, 2011; Cui, Hou, *et al.*, 2010), we expected to find a higher predicted connectivity between fragments of the breeding range than within the wintering range. We further predicted the temporal variation in connectivity within the breeding grounds to be higher than within the wintering grounds. Overall, we want to demonstrate how environmentally informed movement models can contribute to creating null hypotheses for the migration of species from the

observations of a limited number of individuals.

Methods

Tracking data and movement model

We used tracking data of bar-headed geese that were originally collected for a broader disease and migration ecology study implemented by the Food & Agriculture Organization of the United Nations (FAO) and United States Geological Survey (USGS). During the years 2007-2009, 91 individuals were caught in three different locations within the species' native range (Lake Qinghai, China; India; West Mongolia). All individuals were equipped with ARGOS-GPS tags which were programmed to record the animals' location every two hours (ARGOS PTT-100; Microwave Telemetry, Columbia, Maryland, USA). The tags collected and transmitted data for $241 \pm 253\,(mean \pm s.d.)$ days, and in total 169′887 fixes could be acquired over the course of the tracking period (see also Table 1 & Hawkes, Balachandran, *et al.*, 2011). Individuals that were tracked for less than a complete year were excluded from the subsequent analyses, which left a total of 66 individuals (Lake Qinghai: 20, India: 20, West Mongolia: 26).

Table 1. A summary of the catching sites and corresponding sample sizes. The number of tracking days and GPS fixes are listed as a mean per individual.

Capture site	**Year**	**sample size** (individuals)	**First fix taken**	**tracking days** median; [25%; 75% quantile]	**GPS fixes** median [25%; 75% quantile]
Lake Qinghai, China	2007	13	Mar 25 – 31	303 [207; 411]	1670 [682; 2565]
	2008	10	Mar 30 – Apr 4	396 [260; 845]	2211 [1341; 3573]
India	2008	17	Dec 10 – 18	129 [92; 401]	2060 [1578; 2714]
	2009	7	Jan 27 – Feb 06	134 [53; 448]	1321 [1107; 3800]
West Mongolia	2008	19	Jul 13 – 15	122 [90; 190]	537 [366; 1312]
	2009	14	Jul 05 – 08	105 [100; 128]	421 [330; 473]

We extracted the parameters required for the eRTG (Technitis, Weibel, *et al.*, 2016) from the remaining tracking data. The eRTG is based on the geometry and the (auto)correlation structure of the observed movement process (Technitis, Weibel, *et al.*, 2016; Technitis, Weibel, *et al.*, in preparation). It uses empirical distributions of step lengths and turning angles, their covariance, as well as their autocorrelation at a lag of one step. In our extension of the eRTG, we use two different movement modes: *stopover behaviour* and *migratory behaviour*. We identified different

movement modes in the data using an expectation-maximisation binary clustering (EMbC, Garriga, Palmer, *et al.*, 2016), which is an approach for the behavioural annotation of animal movement data. We clustered our locations by speed and turning angle, and retained two clusters: high-speed movements (mean ± s.d.: $8.4 \pm 6.7 m/s$) and movements with low speeds (mean ± s.d.: $0.3 \pm 1.0 m/s$). We used the locations classified as the latter for the stopover mode, and the locations classified as high-speed for the migratory mode (see Figure S2). Estimates of speed and turning angle, however, are highly dependent on the sampling rate of the data. Due to these restrictions, we only used those parts of the trajectories that had no missing data (i.e. only subsequent fixes with a lag of 2 hours).

We also determined the parameters that mediated the transitions between these two movement modes directly from the tracking data. We first identified seasonal migration events between breeding and wintering grounds (and vice versa) in the empirical trajectories using the behavioural annotation. We then determined migratory bouts (sequential locations classified as migratory behaviour) as well as stopovers (sequential locations classified as stopover behaviour, with a duration $> 12h$). We used two main proxies to characterise migratory bouts, namely cumulative migratory distance as well as duration, and one proxy to characterise stopovers, namely stopover duration. We calculated these proxies for all individuals and migrations, and determined the maximum observed distance (dm_{max}) and duration (Tm_{max}) of a migratory bout. As we did not distinguish between extended staging from use of stopover locations during migration, we calculated the 95% quantile of the observed stopover durations (Ts_{max}) rather than the maximum. When simulating a conditional random trajectory between two sites a and b, the eRTG initially draws from the parameters for the migratory mode, producing a fast, directed trajectory. To determine the time allowed for migration between a and b, we assumed the mean empirical flight speed derived for the migratory mode. After each iteration, the cumulative distance of the trajectory (dm) as well as the duration (Tm) since the origin of the migratory bout were calculated. By using dm, Tm, as well as the empirically derived dm_{max} and Tm_{max}, the simulation performs a binomial experiment with two possible outcomes: switch to stopover behaviour with a probability of p_{ms}, and resuming migration with a probability of $1 - p_{ms}$. We defined p_{ms}, the transition probability to switch from migratory to stopover mode, as

$$p_{ms}(t) = \frac{\sum_{i=0}^{t}(dm)}{dm_{max}} \times \frac{\sum_{i=0}^{t}(Tm)}{Tm_{max}} \tag{5}$$

At each step t, the simulation of migratory movement switches to the unconditional stopover mode with a probability of $p_{ms}(t)$. Likewise, the simulation can switch back from stopover mode to migratory mode with the probability $p_{sm}(t)$, which is determined by the duration of the simulated stopover (Ts) and the empirical Ts_{max}. We defined the transition probability from stopover to migratory mode as

$$p_{sm}(t) = \left(\frac{\sum_{i=0}^{t}(Ts)}{Ts_{max}} \right)^2 \tag{6}$$

This process is then repeated until the simulation terminates, which can be due to two different reasons: either the trajectory reaches its destination, or because there is no possibility to connect the two sites a and b within a certain duration $t_{a,b}$ while adhering to the geometric properties of the empirical movement data. With every step that has already been simulated, the degrees of freedom decrease, and so it can happen that a trajectory cannot reach the destination within the specified time, resulting in a dead end.

Simulation and assessment of random trajectories

To choose start- and endpoints for the simulated migrations, we used the range data provided by BirdLife International and NatureServe (2013). According to this dataset, the area occupied by bar-headed geese consists of four distinct breeding range fragments (corresponding to breeding populations, Takekawa, Heath, *et al.*, 2009) as well as four distinct wintering range fragments (Figure S1). We sampled ten random locations from each of these range fragments as start- and endpoints for the simulation of migrations. Using the modified eRTG, we simulated 1000 trajectories for all pairs of range fragments (100 trajectories per sampled location) and counted the number of successes (trajectory reached the destination) and failures (trajectory terminated in a dead end). We then assessed all successful trajectories and estimated their ecological likelihoods in the following way: Initially, we determined the total duration of the migration of trajectory j between locations a and b, $t_{a,b,j}$, the number of stopover sites used, $n_{a,b,j}$, as well as the time spent at each stopover site (δ_k for stopovers $k \in 0, 1, ..., n_{a,b,j}$). We determined the habitat suitability of stopover sites using temporally explicit habitat suitability landscapes. These landscapes were derived from habitat suitability models and time series of remotely sensed environmental information (see Section A in the Electronic Supplementary Material (ESM) for

details). We incorporated seasonal changes in the environment as well as changes in the habitat use of bar-headed geese into the estimates of habitat suitability using a segmentation-by-habitat-use approach (van Toor, Newman, *et al.*, 2016). This method uses animal location data and associated environmental information to identify time intervals for which habitat use is consistent. We used the segmentation by habitat use to determine the number of suitability landscapes that were necessary to reflect differences in habitat use throughout the year. The segmentation by habitat use suggested five temporal segments for bar-headed geese, and so we used the segmentation to derive five distinct habitat suitability models, and the respective spatial predictions of habitat suitability. These segments corresponded to winter/early spring, mid-spring, late spring/summer, early autumn, and late autumn (see Figure S3 & Section A in the ESM for details). We annotated all relocations corresponding to a single stopover event k with the corresponding suitability values for each of these five suitability landscapes. We then calculated the benefit gained by the use of stopover locations using the mean suitability for each of the stopover locations, S_k, and the duration spent at stopover events, δ_k, (see Equation 2). By using five different suitability landscapes, we could derive multiple estimates of stopover benefits, each corresponding to a different time of the year (Figure S3).

To calculate the ecological likelihood for a trajectory j between sites a and b, we also required an estimate for $\tau_{a,b}$, or the time that is necessary for an individual to fly from a to b without the utilisation of stopover sites. We used a simple linear model to predict flight time as a function of geographic distance which we trained on the empirical data derived from the migratory bouts (see Section B in the ESM). By basing the model on the empirical migratory bouts rather than mean flight speed, the estimate for the time necessary to fly from a to b maintains the inherent "wigglyness" of waterbird migrations. For each simulated trajectory, we then calculated the geographic distance between its start- and endpoint, and predicted the estimated flight time $\tau_{a,b}$. Finally, we calculated the ecological likelihood for all trajectories for the different suitability landscapes using equation 4.

To test our hypothesis about differences in connectivity across the breeding and wintering range, we differentiated between ecological likelihood among breeding range fragments (breeding range connectivity), among the wintering range (wintering range connectivity), and between breeding and wintering range fragments (mixed connectivity). For each trajectory, we calculated the median ecological likelihood across all suitability landscapes. We then computed 95%

confidence intervals (CI) of the median and 95%-quantile of the ecological likelihood for these three subsets of the data using bootstrapping (1000 replicates). We tested our hypothesis about temporal variability in predicted connectivity across ranges in a similar way. We calculated the standard deviation of the ecological likelihood for all suitability landscapes on a per-trajectory basis. We then determined the 95% CIs on the standard deviation for the breeding range, the wintering range, and between breeding and wintering ranges separately, again using bootstrapping (1000 replicates).

Deriving a MELC network

We derived a simplified migration network by summarising all simulated trajectories between pairs of range fragments. We calculated both the median and maximum ecological likelihood over all trajectories and suitability landscapes to represent median and maximum connectivity between range fragments. In addition, we calculated confidence intervals for the median ecological likelihood per suitability landscape via bootstrapping (1000 replicates) to estimate the temporal variability of connectivity.

Ecological likelihood of empirical trajectories

We also calculated the ecological likelihood of migrations observed in the tracking data ($n = 179$). Here, we distinguished between autumn ($n = 63$) and spring migrations ($n = 116$), and used the suitability layer that corresponded to the respective date of observation to determine stopover suitability. To put the ecological likelihood of simulated trajectories into a biological context, we calculated 95% confidence intervals on the median of the empirical ecological likelihood using bootstrapping (1000 replicates).

Results

Ecological likelihood of empirical and simulated migrations The simulations resulted in a total of 30′730 simulated trajectories, of which 29.1% connected breeding range fragments (8′945 trajectories, success rate: 74.5%), 17.5% connected wintering range fragments (5′393 trajectories, success rate: 44.9%), and the remaining 53.3% connected breeding and wintering range fragments (16′392 trajectories, success rate: 51.2%; see Figure S4). While these trajectories were successful in

connecting origin and destination, they differed profoundly in their predicted ecological likelihood, which ranged between 0.014 and 0.59. We found that simulated migrations had a higher ecological likelihood for late spring and summer than for autumn (Figure 2).

This was comparable to the range of ecological likelihood of the empirical migrations (0.01 − 0.38). Overall, we found that the estimated ecological likelihood for empirical migrations was higher during spring (eli: [0.0614; 0.1070]; 95% confidence intervals on the median) than during autumn (eli: [0.0270; 0.0514]; 95% confidence intervals on the median). This was caused by differences in the suitability landscapes underlying the calculation of the ecological likelihood of migrations, but also by the differences in migration duration between spring and autumn. We found that bar-headed geese on average stayed longer at stopover sites during autumn than during spring migrations (spring: 6.8 ± 14.2 days, autumn: 11.8 ± 12.2 days; mean ± s.d.).

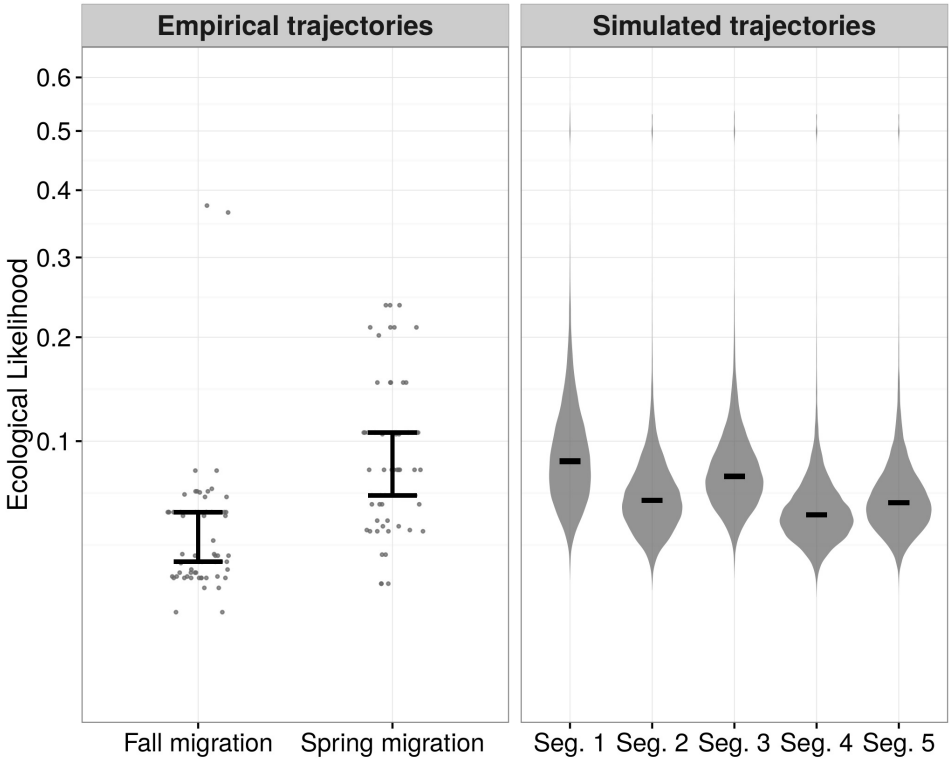

Figure 2. The estimated ecological likelihood (*eli*) of empirical and simulated migrations. Here we show the *eli* for spring and autumn migrations, as well as the *eli* for the simulated trajectories for all suitability landscapes. The black bars show the 95% CIs for the respective medians, and the grey dots and violin plots show the observed (empirical trajectories) and densities for the observed ecological likelihood (simulated trajectories).

Estimated connectivity within the species' range We separated the simulated trajectories into movements within the breeding range, movements within the wintering range, and movements

resembling seasonal migrations between the breeding and wintering range. Here, we found that ecological likelihood of trajectories was highest within the breeding range (95% CI on median: [0.0676; 0.0684] and 95%-quantile: [0.1469; 0.1546]), and lowest within the wintering range (95% CI on median: [0.0590; 0.0596] and 95%-quantile: [0.1090; 0.1147]), predicting that movements between range fragments should occur more often within the breeding than in the wintering areas. The median ecological likelihood for migrations between breeding and wintering range fragments was intermediate (95% CI on median: [0.0618; 0.0622] and 95%-quantile: [0.1224; 0.1296]). These patterns are reflected in the simplified migration network (Figure 3). We also identified the single trajectory with the maximum ecological likelihood between range fragments rather than the median (Figure S5). This maximising migration network predicts that migrations that connect the breeding and wintering ranges have the highest ecological likelihood. Finally, the number of stopover locations of movements was proportional to the geographic distance between range fragments (Figure S6).

Temporal variability of within-range connectivity We found that the spatial patterns of estimated connectivity varied across the suitability landscapes derived from the five detected niche segments (Figure 4; see also Figure S3 for the temporal correspondence of niche segments). For the suitability landscapes derived from Segments 1 (winter), 2 (early/mid spring), and 3 (late spring to summer), the estimated connectivity predicts that bar-headed goose migrations are most likely to occur between the wintering and breeding range, and within the breeding range. For Segment 4 (early autumn), connectivity patterns predict that movement should be most likely between breeding and wintering areas. For late autumn (Segment 5), we also observed that connectivity predicts movement within the wintering range of the species. We also calculated the confidence intervals for the overall ecological likelihood per suitability landscape (Figure 2), which predicts the highest median likelihoods for the periods from Mid-November to the end of February (Segment 1) as well as from Mid-April to Mid-August (Segment 3).

In this context, we also compared the variation of ecological likelihood across suitability landscapes and found the highest variation for the breeding range (95% CI on the median standard deviation: [0.0124; 0.0133]) and the lowest variation for the wintering range (95% CI: [0.0041; 0.0046]). Again, the trajectories between breeding and wintering range fragments showed intermediate values (95% CI: [0.0084; 0.0089]).

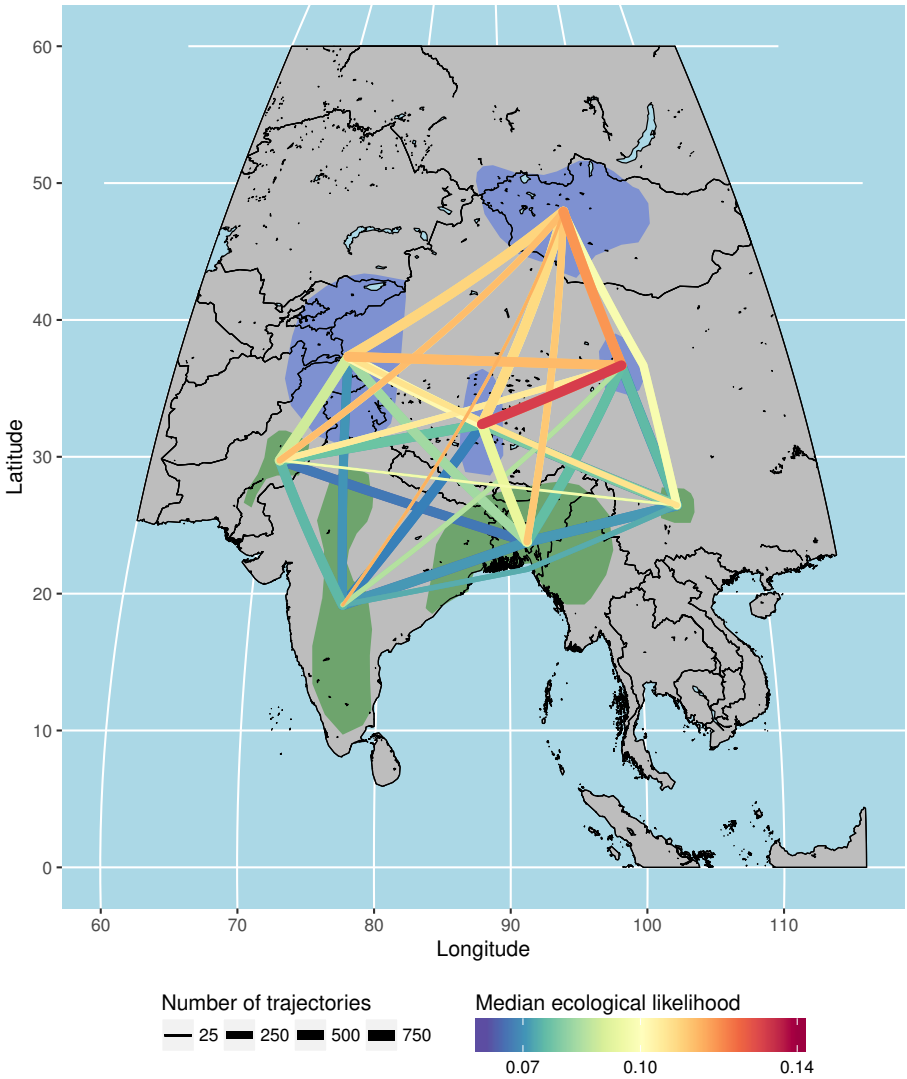

Figure 3. The median connectivity between range fragments of bar-headed geese. We summarised the ecological likelihoods for all pairwise range fragment trajectories using the median ecological likelihood. The thickness of edges represents the sample size. Blue polygons show the native breeding area of the species, green polygons the native wintering range. Long edges are curved for sake of visibility.

Discussion & Conclusions

The increasing availability of high-resolution tracking data has advanced the development of models allowing us to quantitatively describe animal movement in continuous time (e.g. Fleming, Fagan, *et al.*, 2015). While these continuous-time models can estimate the underlying process that has led to the discrete-time observations, they often remain oblivious to the environmental context of the observed behaviour (but see Morales, Haydon, *et al.*, 2004). In this study, we combined realistic movement simulations with a measure of their ecological likelihood and

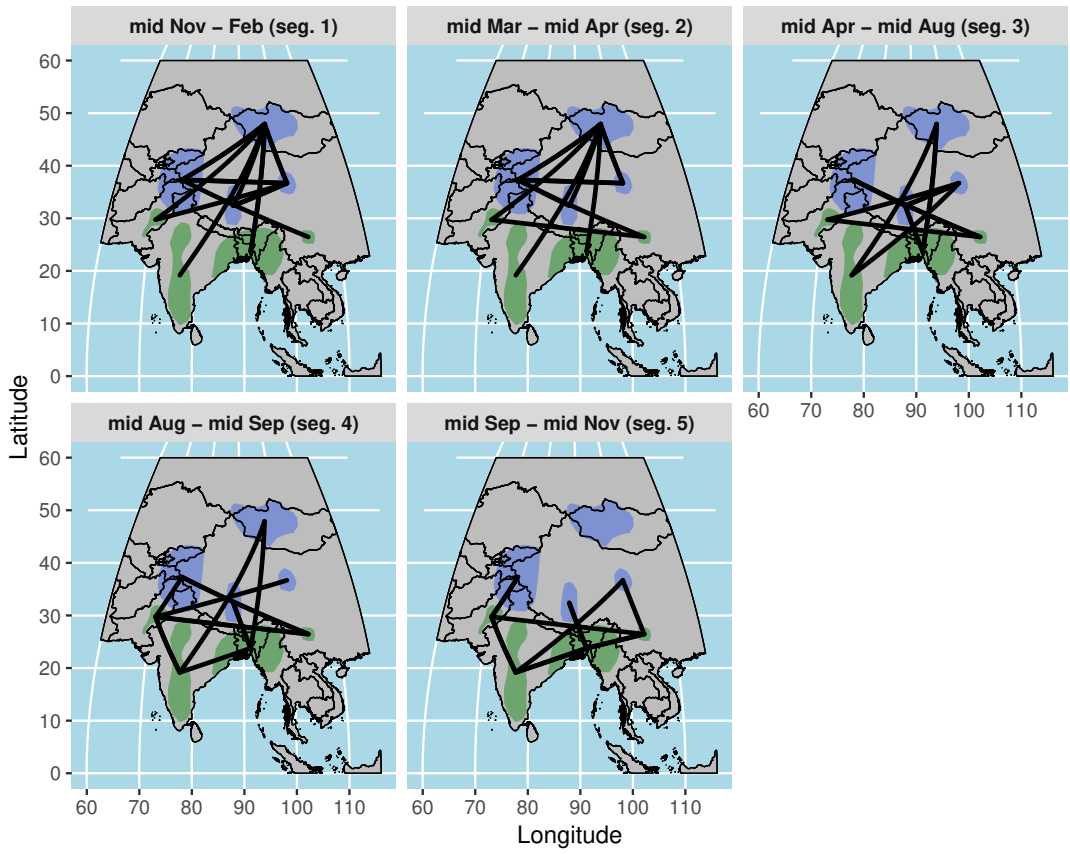

Figure 4. Here we illustrate the temporal dynamics of the predicted connectivity by showcasing the predicted movements for each suitability landscape separately. The visible edges of the network have a median ecological likelihood that is higher than 75% of the ecological likelihood for the complete network. The respective time periods associated to these networks is displayed in Figure S3.

thereby presented a flexible approach to estimate landscape connectivity that is informed by movement and the suitability of the environment. This post-hoc evaluation of simulated trajectories allowed us to derive a MELC network and to predict patterns of connectivity throughout the species range of bar-headed geese, though these results depend on the quality of the provided distribution data of the species. By using simple stochastic transitions between two modes of movement, we could simulate migrations that matched empirical trajectories in their key characteristics such as stopover duration (Figure S7), resulting in an overall similar ecological likelihood of empirical and simulated trajectories.

We found that the predicted connectivity was higher within the species' breeding range than in the wintering areas, confirming the expectations from the literature (Cui, Hou, *et al.*, 2010; Kalra, Kumar, *et al.*, 2011; Bridge, Kelly, *et al.*, 2015). While bar-headed geese are thought to be philopatric to their breeding grounds (Takekawa, Heath, *et al.*, 2009), the post-breeding period

seems to be a time of great individual variability and extensive movements (Cui, Hou, *et al.*, 2010). This has also been observed for other Anatidae species (e.g., Gehrold, Bauer, *et al.*, 2014), as due to the temporary flightlessness during moult the choice of suitable moulting sites is critical to many waterfowl species. As the predicted connectivity within the breeding range and during the summer months is high, we think that unsuccessfully breeding bar-headed geese and individuals in the post-breeding period are not limited by sufficiently suitable stopover sites when moving between breeding range fragments. Furthermore, by using temporally explicit predictions of habitat suitability, we were able to investigate how seasonal changes in habitat use and the environment influence the estimation of ecological likelihood. Our results confirmed that the temporal variability of connectivity is higher in the breeding areas in the North than in the subtropical wintering areas.

Our results show both how our predictions match the expectations of a higher variability of connectivity within the breeding range, but also highlight the importance of integrating temporal variation into measures of landscape connectivity. As Zeigler and Fagan (2014) already pointed out, the ecological function of landscape connectivity through animal movement is not only determined by *where*, but also *when* the environment provides the conditions that allow an individual to move from a to b. This is apparent in cases such as the spread of a disease through a metapopulation, as has happened with the white-nose syndrome in North American bats (Blehert, Hicks, *et al.*, 2009; Turner, Reeder, *et al.*, 2011), and with several subtypes of highly pathogenic avian influenza A virus (e.g. Gaidet, Cappelle, *et al.*, 2010; Newman, Hill, *et al.*, 2012). While in theory the temporal dynamics of landscape connectivity can also be investigated by different means, e.g. cost- and resistance-based approaches like least-cost paths or CircuitScape (McRae, Dickson, *et al.*, 2008), we suggest that in species like the bar-headed goose such traditional models are not easily applicable for several reasons: as a species that mainly moves by powered flight, resistance surfaces to waterfowl migration cannot easily be modelled as a function of environmental features. Contrary to soaring birds, for which resistance surfaces can be modelled using predictors of uplift (Kranstauber, Barber, *et al.*, in preparation), waterfowl do not depend on thermals for locomotion. Furthermore, while wind conditions influence the speed of migrating individuals (Safi, Kranstauber, *et al.*, 2013), the contribution of stopover periods to the duration of migration is much larger than the actual flight time (Hawkes, Balachandran, *et al.*, 2011). Finally, the use of cost-based approaches would also assume an a priori knowledge of stopover locations

and conditions. By combining a movement model with an environmental predictor of habitat suitability, however, we can replicate realistic migrations and evaluate individual trajectories even for populations where stopover sites are unknown. In contrast to cost-based approaches, our method requires less complete knowledge about potentially used stopover locations, and only movement data are necessary to derive the parameters needed for the model. In addition to estimating likely routes, this also gives us information about the temporal dimension of connectivity in terms of how long it takes an individual to move from a to b, and by using dynamic predictors of habitat suitability also in terms of temporal changes in both habitat use and the environment.

While we designed the concept of the MELC for the stepping-stone migration of bar-headed geese or similar species, the approach is applicable to many different scenarios. In our study, we determined the ecological likelihood of trajectories solely via the stopover behaviour, while other measures such as wind support during the migratory mode could easily be incorporated. Similarly, the transition probabilities that mediate between movement modes can be extended to include environmental conditions, because e.g. cold spells can influence an individual's movement decisions (Sauter, Körner-Nievergelt, *et al.*, 2010). This simple set-up performed reasonably well in replicating the movement behaviour observed from recorded tracks, but algorithms such as state-space models could additionally be integrated to simulate animal movement with a more complex configuration of movement modes (Morales, Haydon, *et al.*, 2004; Patterson, Thomas, *et al.*, 2008). Overall, we think that the combination of simulating trajectories with an element of randomness, and environmental correlates for an integrative measure of landscape connectivity like the MELC can be used to establish null hypotheses of migratory connectivity within a species' range. While connectivity estimates derived from cost-based approaches have been successfully used in e.g. population genetics (Row, Blouin-Demers, *et al.*, 2010), for events that happen on smaller temporal scales, such as e.g. seed dispersal, it is of higher importance to not only estimate likely routes, but also the temporal component of movement. Thus, using models that incorporate a species' movement behaviour provides estimates for landscape connectivity for a wider range of applications. While the eRTG emulates the geometry of the observed movement path with a given duration and end point, the use of methods that estimate temporally explicit utilisation distributions can derive more continuous measures of space use (e.g. Kranstauber, Kays, *et al.*, 2012; Kranstauber, Safi, *et al.*, 2014).

As the movement of animals can be driven by internal and external factors influencing an individual's decisions (Nathan, Getz, *et al.*, 2008), there are many non-exclusive explanations for how, when, and why the individual moves. With the miniaturisation and decreasing cost of tracking technology, it is becoming possible to describe animal behaviour in unprecedented detail for many individuals and species. However, the direct transferability of the acquired knowledge to different populations or seasons remains challenging. The necessity to establish null models of e.g. how animals move through a landscape, or at which time they decide to initiate migration, is thus more urgent than ever (Nathan, Getz, *et al.*, 2008). In the light of migratory animals and their potential role as vectors for pathogens, seeds, or invasive species, the understanding of connectivity networks and the mapping of the probability space of movement are of crucial importance. Especially in areas where our understanding of migrations is limited, our method can be used to quantitatively predict potential flyways from empirical movement data, and can so complement empirical knowledge (e.g., Palm, Newman, *et al.*, 2015). Such predictions could in turn be used to inform e.g. risk models. The MELC provides a starting point for complementing tracking efforts with ecologically relevant estimates of a species' potential to migrate and act as a link between patches, populations, and ecosystems.

Acknowledgements

This work was made possible by the efforts of the many cooperating scientists in China, India, and Mongolia who assisted the Wildlife Health and Ecology Program at the Food and Agriculture Organization of the United Nations (FAO) and US Geological Survey (USGS) in the collection of the tracking data with ecological findings provided in other reports and papers. We are indebted to Markus Rampp and Karin Gross at the Computation Center of the Max Planck Society for their support with the computational facilities. The use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the US Government or FAO. The views expressed in this publication are those of the author(s) and do not necessarily reflect the views or policies of the FAO or the US Goverment. This study reanalysed several datasets from FAO and USGS published studies; Institutional Animal Care and Use Committee details are available in the original publications. MLvT was supported by the International Max Planck Research School for Organismal Biology.

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