Movement of juvenile migratory birds from settlement to adulthood across the non-breeding range

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Abstract

1. Among migratory vertebrates, high levels of fidelity to non-breeding sites during adulthood are common. If occupied sites vary in quality, strong site-fidelity can have profound consequences for individual fitness and population demography. Given the prevalance of adult site-fidelity, the regions of the non-breeding range to which juveniles first migrate, and the scale of any subsequent movements, are likely to be pivotal in shaping distributions and demographic processes across population ranges.

2. However, inherent difficulties in tracking migratory individuals through early life mean that opportunities to quantify juvenile settlement and movements across non-breeding ranges, and the mechanisms involved, are extremely rare.

3. Through long-term, range-wide resightings of hundreds of colour-marked individuals from their first migration to adulthood, and application of state-space models, we quantify levels of juvenile and adult regional-scale movements and distances at different life stages across the whole non-breeding distribution range in a migratory shorebird, the Black-tailed Godwit (*Limosa limosa islandica*).

4. We show that the probability of individuals changing non-breeding regions (seven historical wintering regions spanning the Western Europe range) at all ages are very low (mean movement probability = 10.9% from first to subsequent winter, and 8.3% from first adult winter to later winters). Movement between regions was also low between autumn and winter of the same year for both juveniles (mean movement probability = 17.0%) and adults (10.4%). The great majority of non-breeding movements from the first autumn to adulthood were within regions and less than 100 km.

5. The scarcity of regional-scale non-breeding movements from the first autumn to adulthood means that the factors influencing where juveniles settle will be key determinants of non-breeding distributions and of the rate and direction of changes in distributions.

Introduction

The processes by which species ranges form and change are of fundamental importance in understanding population responses to environmental change, as well as the continued effectiveness of site protection strategies, but understanding the dynamics of species distributions remains a fundamental challenge in ecology and conservation (Gunnarsson et al. 2005a, Maclean et al. 2008, Planes et al. 2009, Hodgson et al. 2011, Alves et al. 2019). Repeated use of space by individual organisms (site-fidelity), will tend to maintain existing distributions, and range chage in systems with strong site-fidelity may be more dependent on shifting patterns of juvenile settlement and/or survival (Gill et al. 2019). Long-lived vertebrates often show remarkably high levels of site-fidelity as adults (Paradis et al. 1998, Phillips et al. 2005, Jorgensen et al. 2010, Gill et al. 2019). For example, migratory birds typically show very high return rates of individuals to both non-breeding and breeding areas (Newton 2010, Paruk et al. 2015, Clark et al. 2016, Méndez et al. 2018a), despite traversing continents on their migratory journeys (Gill et al. 2009, Alves et al. 2016). Site-fidelity can therefore be a major force shaping the distributions of migratory populations over large spatial scales (Winger et al. 2019). Rapid range expansions are occurring in many migratory systems at present (Keller et al. 2020, Rushing et al. 2020) and, in the light of strong adult site-fidelity, the movement and settlement patterns of juveniles are likely to be key in shaping such large-scale changes in spatial distributions, but very little is known about this process (Gill et al. 2019, Battley et al. 2020).

In migratory systems with strong adult site-fidelity, high levels of exploratory movements at the juvenile stage could facilitate both aggregation of individuals in higher quality non-breeding areas and rapid responses to shifting environmental conditions. Alternatively, exploratory movements by juveniles, within the first region they encounter when arriving at the non-breeding grounds, or between regions, may be more limited in distance and/or frequency, in which case the factors influencing the probability of juveniles migrating to different locations in their first autumn (and their subsequent rates of survival) would be major drivers of population distribution. The relative importance of juvenile exploratory movement and settlement in shaping patterns of local aggregation across migratory ranges is likely to have profound consequences for conservation, as site protection is typically based on numbers of birds using sites (Méndez et al. 2018b). If juvenile exploratory movement is limited and adult site-fidelity is strong, local populations may also be more vulnerable to the impacts of environmental change in the areas that they occupy (Burton et al. 2006, Goss-Custard et al. 2006).

Understanding individual site-fidelity and movement at different life stages is also important because of the potential implications for survival of occupying sites that vary in quality and resource availability (Alves et al. 2013, Carneiro et al. 2021). Strong site-fidelity could result in individuals occupying locations with relatively poor conditions (in non-breeding and/or breeding locations), even when better quality conditions are available elsewhere in the range. If individuals in migratory populations are more likely to occupy either higher or lower quality locations in both winter and summer, site-fidelity to these locations can introduce stronger fitness variance than single-season effects. This could influence both effective population sizes, and thus vulnerability of populations (Gunnarsson et al. 2005a), and distributions through spatial variation in survival rates (Gill et al. 2019). If the probability of individuals settling in any given location across a range is random, such seasonal matching of habitat quality would be less likely to occur. However, if individual settlement is non-random, for example if migratory directions and/or distances vary with early life experiences (Teitelbaum et al. 2016, Loonstra et al. 2020) and/or with social or environmental conditions experienced before or during migration (Trierweiler et al. 2014, Meyburg et al. 2017), then systematic links between breeding and non-breeding sites may arise. In a few migratory systems, juveniles travel with their parents and typically adopt the parental wintering distribution, likely creating strong migratory connectivity (Schamber et al. 2007, Newton 2010, Méndez et al. 2021, Byholm et al. 2022). In these systems, juvenile settlement in non-breeding areas will be predictable and highly structured, and juvenile distributions will resemble parental distributions (Harrison et al. 2010). However, in most migratory bird species, juveniles travel independently of their parents and will have to use other cues for settlement than following parents (Gunnarsson et al. 2005a, Newton 2010, Skórka et al. 2016). While parental guidance on migration is relatively rare, other social factors, such as travelling in flocks or with more experienced individuals, may be a common route for transmission of social information (Simons 2004, Couzin et al. 2005, Tombre et al. 2019, Méndez et al. 2021, Byholm et al. 2022). To evaluate the contribution of juvenile movement and settlement to population distributions and individual fitness, longitudinal data on individual movement histories from initial settlement to adulthood are needed at population- and range-wide scales.

Icelandic Black-tailed Godwits (*Limosa limosa islandica*) are large migratory shorebirds that breed almost exclusively in Iceland and winter across Western Europe (Gill et al. 2001). Godwits, like most shorebirds, migrate independently of their parents (Gunnarsson et al. 2005a) and typically take two years to reach maturity and return to their breeding grounds (Gunnarsson et al. 2012). This population

has been the subject of a range-wide mark-resighting study of individually marked birds since 1995. With the help of over two thousand volunteer observers, marked individuals have been tracked across the entire migratory range (Alves et al. 2010, Gill et al. 2014). Over 1200 juveniles have been marked in Iceland since 1999, many of which have subsequently been tracked across repeated migrations. In order to quantify levels of individual movement and patterns of settlement during the first years of life, here we use state-space modelling of the nn-breeding locations of individuals tracked across the non-breeding range to quantify: 1) probabilities of individuals moving between non-breeding regions within and between years, 2) variation in these probabilities across life stages spanning first autumn to adulthood, and 3) individual movement distances between these life stages.

Methods

The annual cycle of Black-tailed Godwits

Icelandic-breeding Black-tailed Godwits winter on the coasts of W-Europe, from Ireland and Britain in the north to Iberia in the south (Gill et al. 2001, Gunnarsson et al. 2005b, Alves et al. 2013). The majority of the population winters in Ireland, Britain, France and Portugal, with small numbers in the Netherlands, Belgium and Spain (Gunnarsson et al. 2005b). Autumn (post-breeding) migration from Iceland takes place from July to September and spring (pre-breeding) migration to Iceland spans April to May (Gunnarsson et al. 2006b, Alves et al. 2012). Adults are highly consistent in their use of a small number (~4-5) of non-breeding sites (individual estuaries or wetlands) throughout their lives, but these sites can be within the same region or spread across regions (and countries) and are typically used at similar times each year (e.g. during autumn, winter and spring; (Gill et al. 2019). Adults undergo a complete body moult during autumn and migratory movements frequently occur from autumn moulting sites to winter sites, and from winter sites to spring passage sites. Juveniles undergo a partial moult through their first autumn and early winter and many juveniles remain in non-breeding sites during their second summer (ie as non-breeding immatures). In Iceland, Black-tailed Godwits are restricted to breeding in lowland areas which are distributed as coastal basins around the country, with most of the population breeding in the South, West and North of Iceland (Gunnarsson et al. 2005b, Gunnarsson et al. 2006a, Johannesdottir et al. 2014, Jóhannesdóttir et al. 2017, Alves et al. 2019).

Individual marking and resighting

Godwits have been caught on the wintering grounds since 1995 and as nesting adults since 2001, and pre-fledged chicks have been caught since 1999, and all have been individually marked with unique combinations of colour-rings (Gunnarsson et al. 2005a, Alves et al. 2013, Gill et al. 2014). With the help of a network of volunteer observers, marked individuals are frequently resighted across the non-breeding range (Gunnarsson et al. 2005a) within and between years. Here we use resightings during the non-breeding season (i.e. outside of Iceland) of 3099 marked individuals; 1264 birds marked as chicks or (recently fledged) juveniles in Iceland between 1999 and 2012, and 1835 birds marked as 3rd calendar year or older in Iceland or in winter between 1995 and 2013.

Population-wide probability of movement between non-breeding regions and periods

In order to estimate the probabilities of moving between seven non-breeding regions (Fig. 1), while accounting for between-region variation in detectability, we developed two state-space models: the first to estimate probabilities of moving betwen non-breeding regions from autumn to winter periods during a single non-breeding season (*autumn-winter* model, incorporating 8822 sightings of 2062 individuals), and the second to estimate the probability that individuals change their wintering regions from one year to the next (*winter to winter* model, incorporating 2949 resightings of 1304 individuals). The autumn-winter models were constructed to capture rates of movement from first arrival on the wintering grounds into the wintering period where initial sampling of sites could potentially take place. The winter-winter models were constructed to capture rates of movement between winter periods, as juveniles typically do not return to the breeding grounds until their second year and so sampling of sites could take place after the first winter period. Our models only used observations made outside Iceland, and we defined the autumn monitoring window as 1 Jul to 14 November, and the winter monitoring window as 15 Nov to 14 Feb for juveniles, and 31 Jan for older individuals. The start of the autumn window (1 Jul) and the end of the winter window (31 Jan, 14 Feb) reflect the earliest autumn-winter movement and latest winter-spring movement of birds from the southern (i.e. most distant from the breeding grounds) part of the range (Alves et al. 2012). The division of regions used in these analyses follows from previous studies of this system (Gill et al. 2001, Gill et al. 2019), and reflects the historical pattern of non-breeding range expansion in this population and the availability of suitable estuarine and wetland habitat. The multistate model approach requires resightings data to be grouped (to control for differences in resighting effort) and regional-scale groupings allow us to

estimate the frequency of large-scale movements while maintaining sufficient data within each 'state' (ie region). Observer effort varies spatially, with sites with few godwits generally being less well-observed but these sites occur in all regions, and our models of movement probabilities allow for variation in sampling effort between regions (see below).

The models were multistate extensions of the classical CJS (Cormack-Jolly-Seber) model (Calvert et al. 2009), where state values 1-7 indicate the 7 wintering regions (Fig. 1) in which living birds spend each monitoring window with the 8th state representing mortality or permanent emigration from the study region (which cannot be differentiated without additional movement data; (Gilroy et al. 2012)).

We encoded the mark-resight data into three matrices: an observation matrix y containing binary indicators of whether each individual i was observed in a given monitoring window t; a partially-observed state matrix z that indicated the region where each observed individual spent that monitoring window (coded 1-7); and a third data matrix g indicated the age of each individual (coded as 1, 2 or 3 for juvenile, second-year or adult, respectively) in each monitoring window. Values of $z_{i,t}$ for monitoring windows where individuals were not observed (i.e. $y_{i,t}$ = 0, 'gaps') were treated as missing data (coded NA) and imputed by the model, with gaps falling between observations being assigned to one of the live states (1-7), and gaps following the last observation for an individual being assigned to either a living state or death/emigration (state 8), determined by the relevant transition, survival and detection probabilities. Ages ($g_{i,t}$) for monitoring windows where individuals were not observed ($y_{i,t}$ = 0) were in-filled manually based on time elapsed since the last observation. In cases where individuals were observed in more than one region within a single monitoring window, we assigned them to the region they were observed in most frequently in that window (or in the case of ties, the first region they were observed in during that window).

We modelled the true states $z_{i,t}$ as a categorical distribution with probabilities given thus:

where the top row represents probabilities associated with transitions between the 7 regions (i.e. K=7), which are dependent on both movement   and survival φ probabilities. The movement probabilities are allowed to differ between each region-region pairing ($a:K$), and also vary between

age classes **g**, while survival probabilities vary only between ages. The second row above represents the probability of transitions to the unobservable state $K+1$ (i.e. mortality or permanent emigration), and the remaining rows ensure that once individuals move into the unobservable state they remain there permanently.

The model requires a further constraint that the movement probabilities **ϑ** for surviving individuals within each age class must sum to 1. Following White et al. (2015), we impose this constraint using a multinomial logit link function, where probabilities of between-region movements are modelled using beta parameters (β^{ab}, β^{ac},…, β^{ak}.) defined thus:

where   is the probability of an individual moving from region a to region b, given its age g at time t. The probability of an individual remaining in the same region is then defined as:

For the autumn-winter model, we estimated separate age-specific movement and survival probabilities for transitions from autumn to winter and also from winter to subsequent autumn periods.

In both models, the observations $y_{i,t}$ were modelled as Bernoulli trials, where the probability of detection of an individual **ρ** depends on the region occupied by each surviving individual (given by its true state $z_{i,t}$), with probabilities defined thus:

where the top row represents detection probabilities for each region and the bottom row dictates that detection is impossible for individuals in the mortality / permanent emigration state.

We define age-specific hyperpriors for all survival and movement probabilities, using non-informative diffuse conjugate normal distributions for parameter means, and gamma distributions for parameter precisions (Calvert et al. 2009). We fitted the models using JAGS 4.3.0, basing our inferences on 1,000 posterior samples for each parameter after an initial burn-in of 10,000 samples, retaining every fifth sample from three chains. The burn-in length was determined using Gelman and Rubin's (1992) potential scale reduction factor, with convergence subsequently being confirmed

using the 'Rhat' statistic (Rhat <1.01 for all monitored nodes) (Gelman and Rubin 1992). We used a posterior-predictive check to assess model fit, calculating the proportion of posterior samples where the summed deviance across observed capture histories (matrix **y**) exceeded the summed deviance of observations simulated from the fitted model, with values of 0.61 for the autumn-winter model and 0.56 for the winter-winter model (values close to 0.5 indicate well-fitting models; (Chambert et al. 2014)). We evaluated the significance of differences in movement probability between age classes by estimating the posterior distributions of differences in mean age-specific movement probability across regions (e.g. $\theta_{age1} - \theta_{age2}$) and inferring significance if >95% of the resulting distribution fell above or below zero.

Individual variation in non-breeding dispersal distances

To quantify the distances moved by individuals and compare distances moved in early life to life-long distances moved, we compared the maximum recorded distance moved by each bird ringed as a juvenile during: (1) first autumn to first winter, (2) first winter to second winter and (3) first autumn to adulthood (≥ second winter). Each of the regions used in this analysis has between 1 and 27 separate sites (Fig. 1), and distances (in km) between the two most distant sites in which each individual was recorded in each of the two periods were measured digitally in Google Earth. To account for non-independence of individuals tracked at different ages a GLMM with a Poisson error structure and a log-link was constructed with movement distance as the response variable, life stage (Table 1) as a fixed factor and individual as a random factor. Movement distances between the relevant time periods were available for 98 individuals in total of which 67 had information for one period, 10 had information for two periods and 21 had information for all three periods considered. The distribution of distances between centroids of the seven wintering regions (midpoint of region) was also measured to quantify the range of possible between-region movement distances.

Results

Probabilities of individuals moving between regions

For the 3099 marked individuals tracked in this study, the average movement probability across all between-region transitions was low (~10%) at all life stages (Table 2), with most individuals using the same wintering region throughout their life (Fig. 2). The median estimated probability of movement between non-breeding regions from autumn to winter within a single year was 17.0% for juveniles

and 10.4% for adults, and did not differ significantly between age (Table 2). Resighting probabilities ranged from 0.221 to 0.573 between the seven wintering regions (Fig. 1).

Distances moved between non-breeding seasons

The distances between the centroids of the seven wintering regions ranged from 246 to 1723 km (mean = 847 km ± 86.4 SE, n = 28) and the maximum distances moved by individuals between seasons were at the lower end of this range. The great majority of individual movements were less than 100 km (first autumn to first winter: median = 15 km ± 63.9 SE, n = 52; first winter to second winter: median = 15 km ± 46.2 SE, n = 50; first autumn to adult winter: median distance = 129 km ± 290 SE, n = 49; Fig. 3) and 21 of these observations involved individuals in the same site in both time periods. Compared to the first autumn to first winter, individuals moved significantly shorter distances between the first and second winters and significantly further during the whole period from the first autumn to adult winter (Table 3), these differences being largely driven by the few individuals that moved large distances (Fig. 3).

Discussion

Using thousands of resightings of hundreds of individuals of different ages across the non-breeding range of a migratory bird population, this study demonstrates that regional-scale changes of wintering locations are not common at any life stage, and the great majority of individuals return repeatedly to the wintering region they have used previously. Between-region movements are slightly more common between autumn and winter within a single non-breeding period, for juvenile and adult stages, potentially reflecting individuals detected during regular autumn stop-overs on a migratory route established in the first year of life. Movement rates of juveniles could be underestimated if some movements from sites with no observers to well-observed sites are common. However, the very high level of coverage of colour-marked godwits across the non-breeding range means, especially on sites supporting large numbers of godwits, makes this very unlikely. In addition, for the few juveniles that did move during the non-breeding season, distances travelled were rarely more than 100 km between the first autumn and first winter periods, the first and second winters or the first autumn and any subsequent winter. Under-recording of these movements would thus have little influence on the estimates of regional-scale movement probabilities. This pattern of limited large-scale movement from the first autumn to adulthood suggests that the factors influencing juvenile settlement patterns,

operating either before or during the initial settlement process, and subsequent survival rates will be key determinants of population distribution.

Understanding the processes influencing population-level responses to environmental change is of critical importance during the current biodiversity crisis (Johnson et al. 2017, Gill et al. 2019). Migratory birds are some of the most mobile organisms on earth and individuals could potentially move between different parts of a range within relatively short time periods, allowing them to sample conditions in differing locations and respond rapidly to changes in environmental conditions by shifting locations (Treirweiler et al. 2013). However, changes in bird population sizes usually result in changes in local abundance rather than changes in site occupancy (Méndez et al. 2018b), and habitat loss has been shown to lead to reduced survival of displaced individuals, suggesting that there are restrictions on, and consequences of, movements away from familiar non-breeding areas (Burton et al. 2006, Méndez et al. 2018b). Limited movement of individuals throughout their lives, as demonstrated in this system, will also mean that the range changes which are occurring in many species at present (Keller et al. 2020, Rushing et al. 2020) are more likely to be driven by generational changes in patterns of settlement across a range (Verhoeven et al. 2018, Gill et al. 2019).

Our models suggest that the majority of godwits remain faithful to their first wintering region for the remainder of their lives, with the majority of individuals (at least 65%) arriving within this region in their first autumn. As regions and sites across the wintering range from Britain to Iberia vary greatly in quality, these initial settlement decisions can potentially have important fitness consequences (Gunnarsson et al. 2005a, Alves et al. 2013). During the 20th century, the breeding and non-breeding ranges of the Icelandic godwit population have expanded, and generational changes in patterns of settlement and/or survival have been identified as the most likely mechanism through which these changes have occurred (Gill et al. 2019). As most juveniles stay in the region encountered during their first autumn, identifying the processes that influence where individuals first settle is likely to be key in understanding patterns of abundance and fitness variation across ranges, as these processes are likely to have an important influence on the population-scale impacts of environmental change (Gill et al. 2019). Recent advances in tracking of migratory birds are revealing the importance of the social environment in determining migratory routes and timings of individuals, both at small and large spatial scales (Mueller et al. 2013, Dhanjal-Adams et al. 2018, Nagy et al. 2018, Méndez et al. 2021). These social factors may therefore be key contributors to the fate of juvenile godwits, through their influence

on first autumn settlement locations and the subsequent life-long consequences (Gunnarsson et al. 2005a, Alves et al. 2013, Gill et al. 2019). Site-fidelity of adult migratory birds to non-breeding sites is typically very high. For waders, annual return rates of ~0.8 are common and approach annual survival estimates, suggesting that most adults are faithful to their non-breeding sites between years (Méndez et a. 2018a). Similar rates, taking annual survival variation into account, for many waterfowl and songbirds suggesting that the patterns described in this study may be very common with important implications for migratory populations (Newton 2010). Very little is known about age-related changes in non-breeding distributions (Newton 2010).

Across the globe, many migratory bird populations are in decline (Runge et al. 2015, Rosenberg et al. 2019). Shorebird populations, in particular, are experiencing the impacts of widespread habitat loss and fragmentation (Pearce-Higgins et al. 2017, Studds et al. 2017). Understanding how individuals respond to change is vital in order to mitigate these impacts. Our study adds to accumulating evidence that individual migratory birds may be poorly equipped to respond to environmental degradation by moving to alternative locations, because of the strong site-fidelity that is common among long-lived species (Burton et et al. 2006, Winger et al. 2019). In Icelandic Black-tailed Godwits, it is evident that the initial settlement process is more important in determining the winter distribution of the population than any subsequent large-scale sampling by individuals. Thus understanding the drivers of juvenile settlement and survival will be key in understanding generational change and its consequences for distribution and abundance.

Table 1. Definitions of the age and stage categories used to explore variation in movement at different life stages of Icelandic Black-tailed Godwits.

Stage	Age code	Definition
First autumn	1	Sightings outside Iceland from 1 July to 13 November in the first year of life.

First winter	1	Sightings from 14 November to 14 February in first winter of life.
Second autumn	2	Sightings from 1 July to 13 November in the 2nd calendar year of life.
Second winter	2	Sightings from 14 November to 14 February in second winter of life.
Adult autumn	3	Sightings from 1 July to 13 November in the 3rd calendar year of life and all subsequent years.
Adult winter	3	Sightings from 14 November to 31 January in the 3rd calendar year of life and all subsequent years.

Table 2. Probabilities of Icelandic Black-tailed Godwits moving between the seven major wintering regions at different life stages, and the associated survival estimates. CY = calendar year.

Model	Age group	Movement probability (95% credible interval)	Annual survival (95% credible interval)[1]
First autumn to first winter	Juveniles	0.170 (0.047-0.359)	0.854 (0.834-0.874)
Second autumn to second winter	2CY	0.087 (0.046-0.163)	0.909 (0.883-0.936)
Adult autumn to adult winter	Adults	0.104 (0.073-0.145)	0.931 (0.927-0.934)
First winter to second winter	Juvenile to 2CY	0.109 (0.038-0.238)	0.699 (0.652-0.749)[1]
Second winter to adult winter	2CY to 3CY	0.032 (0.004-0.105)	0.759 (0.695-0.819)[1]
First adult winter to later winters	3CY and older	0.083 (0.049-0.128)	0.802 (0.788-0.815)[1]

[1]In the winter-winter model where only winter sightings are used, apparent survival may be underestimated due to removal of observations from other time periods.

Table 3. Results of a GLMM of the variation in maximum distances moved by individuals at three life stages.

Response	Predictors	Estimate	SE	t-value	P
Distance	Intercept	3.596	0.235	15.26	**< 0.001**
	First autumn – First winter				
	First winter – Second winter	-0.656	0.026	-25.0	**< 0.001**
	First autumn – Adult winter	0.132	0.015	8.63	**< 0.001**

Figure 1. Map of the wintering range of Black-tailed Godwits showing sites from which mark-resight data were collected, categorised (colours) into wintering regions between which movement was estimated. Sample sizes (N) show numbers of unique individuals resighted at least once during autumn or winter periods in each region, together with median annual resight probabilities (p) derived from the CJS model.

Figure 2. Median estimated probabilities of individuals moving between non-breeding regions (a) within and (b) between years, across three life stages (left: 1s Year; middle: 2nd Year; right: Adult). Colours indicate median posterior probability estimates from separate multistate models for (a) within-year autumn-winter transitions and (b) between-year winter-winter transitions. Probabilities of remaining within each region is also shown numerically in the diagonal for each age class.

Figure 3. Maximum recorded distances moved by individual Black-tailed Godwits between locations in each of three key life-stages; black: first autumn to first winter, n = 52; dark grey: first winter to second winter, n = 50 and pale grey: first autumn to adult winter, 3rd or any subsequent winter, n = 49.

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