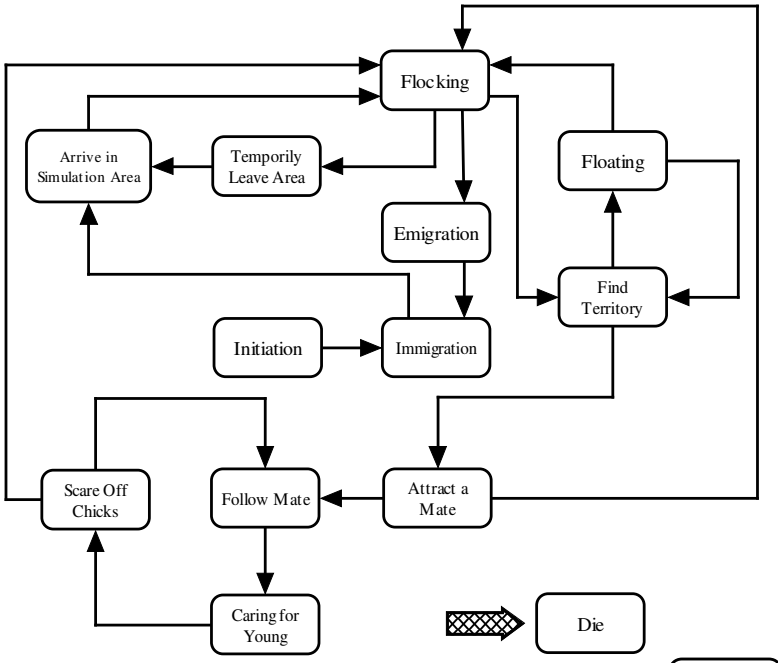
Skylark Model Description

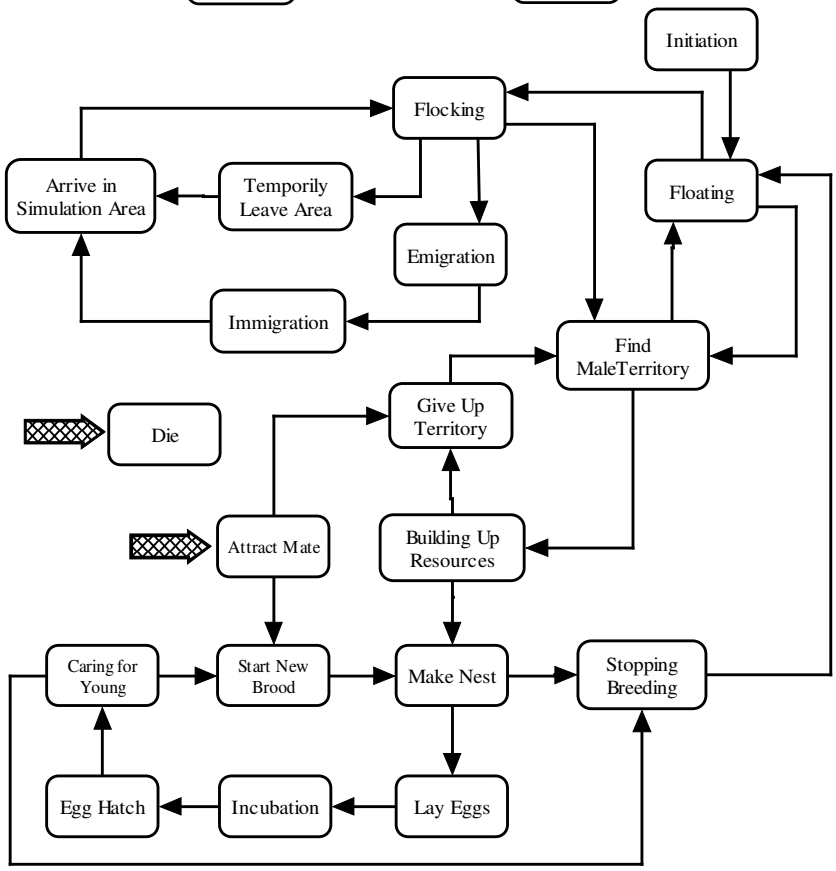
The skylark model simulates the ecology and behaviour of the skylark (*Alauda arvensis*) in Denmark. The skylark is a passerine bird, originating in steppes and thus preferring an open habitat for breeding. It is a common bird in agricultural areas in Denmark. Its food is both plant and arthropods, but it relies on arthropods during the breeding season, and for feeding the young.

Skylark Adult State/Transition Diagrams

Male



Female



Development - of nestlings and eggs is a complicated issue and therefore is described in more detail here.

The model parameters related to reproduction and development are shown in Table 1. The egg-cooling rate (ECR) during periods of inattentiveness is for isolated eggs in still air and includes heat loss due to radiation, convection and evaporation of moisture through eggshell. Development rate of the eggs and young is controlled by the rate of feeding by the adults. In the eggs this is determined by the amount of time incubated, which is related to the length of time required for the female to obtain enough food to cover her existence metabolism requirements (EMA). During periods of inattentiveness the eggs cool, and are then warmed up again on the bird's return. The impact on development of the eggs is thus assumed to be:

$$md = \left(\left(\frac{(IT - Tb)}{2} \right) + Tb \right) \times I$$

where *md* is minute degrees, *IT* is the incubation temperature, *Tb* is the lowest temperature reached during cooling, *I* is the period of inattentiveness in minutes. Eggs sum minute degrees until the development total (DI) is reached. Nestling growth is determined by the rate of feeding of the adults up to a maximum growth rate determined by the maximum growth rate found in field data (MGR) [1]. Conversion efficiencies of dry-weight of insects to bird body weight were obtained from data from the house sparrow (*Passer domesticus*) [2]. This data was scaled proportionally for the differences in skylark weight and time taken for growth until adult weight. Bad weather such as cold, wet or windy days (CD, WD, & WID) result in the female skylark spending time keeping the nestlings warm. Since 'Bad weather' is a categorical variable, the time used was assumed to be half the day. This was deducted from the time available for foraging. The extraction rate (ER), of food from habitats is a scaling parameter that was used to adjust the rates of development such that all eggs, nestlings and fledglings developed at the correct rate according to field data [1]. This same field study provided data on overall mortality rates of eggs and nestlings, which was used to adjust daily predation rates of eggs and nestlings (EMP, NMP) in order to obtain these overall figures. Starvation mortality was assumed when the nestlings did not obtain their existence metabolism (EMJ) for two days running. Mortality of eggs was assumed if development took longer than 14 days (field data observed maximum before desertion of the female).

States

Initiation
The skylark enters the simulation as an adult. Immediate transition to floating.

Floating
The bird moves around the simulation area continually trying to find vacant territories of suitable quality via regular transition to Find Territory. If the end of the breeding season is reached, then there is a transition to flocking.

Find Territory – Male
The determination of the territory positions and sizes is complicated. The model achieves this through a pre-processing of the landscape on the day in the year that the first bird returns. This pre-processing determines where in the landscape territories can physically fit, and places them ready for the returning birds to select from. Pre-processing is based upon habitat quality criteria related to the height of vegetation and habitat types, and results in a density of skylark territories

per 100Ha. Vegetation height in potentially suitable habitats was evaluated based on nesting acceptance criteria (VQ in Table 1). Selection of these territories is based upon the nesting suitability at the time of evaluation; hence, what was a good territory early in the year may be poor later due to vegetation growth (e.g. if planted with winter rape). The result of pre-processing is that territories are therefore fixed each year, and unlike real territories cannot vary in size or shape throughout the season, but may continually change their occupancy status as the season progresses. The male bird therefore assess territories for acceptance as he moves through the landscape. When he finds a suitable territory he will discontinue searching and make a transition to attract mate. An older male skylark can remove a younger male from his territory if that male is not already paired.

Emigration
The birds are assumed to be in their over-wintering areas. Date and weather conditions are checked until they are suitable for immigration, at which time there is a transition to Immigration.

Immigration
On entry to immigration there is a probability test for over-wintering mortality. This test is sex and age dependent. Afterwards there is an immediate transition to Arrive in Simulation Area.

Arrive in Simulation Area
A position in randomly chosen for the bird, after which it makes a transition to flocking.

Flocking
The bird is assumed to move around the area waiting until weather conditions are suitable to begin Find Territory or Emigration, depending upon the time of year. If before breeding, and weather conditions deteriorate (heavy wind or rain, or snow cover), then there is a transition to Temporarily Leave Area. Otherwise if conditions are good (low ind, low rainfall, and temperature >5°C) There will be a transition to Find Territory. If after breeding, then poor conditions will trigger a transition to Emigration. A transition to Emigration will also occur if the bird has not emigrated until October.

Temporarily Leave Area
The bird is removed from the simulation area until there have been three consecutive days of temperatures above freezing, after which there is a transition to Arrive in Simulation Area.

Scare off Chicks
When the chicks reach 30 days old then they are scared out of the territory by the male.

Follow Mate (Male)
The male occupies the same location as the female. When the female's eggs hatch there is a transition to Caring for Young. If the female dies or abandons the territory, there is a transition to Attract a Mate.

Attract a Mate (Male)
The male waits for a female to select and accept his territory. If the breeding season comes to an end, there is a transition to flocking. If a female arrives, there is a transition to follow mate.

Die
Remove the skylark from the simulation. Ensure any dependent skylarks are told that the bird has dies (mate, and/or young).

Find Territory - Female
This behaviour is the same as Find Territory - Male, except that the female looks for territories containing males trying to attract a mate. If her previous mate is present, she will assess his territory first.

Caring for young - Male/Female
Males and females use the time available to them for foraging to obtain food resources from their home range. These resources are then reduced by the existence metabolism of the bird, the remainder is then fed to the chicks in lots corresponding to hourly feedings. Feeding is even between chicks if there is sufficient food to satiate all chicks - if less food is available, the largest chick will obtain the food. Males stay in this state until the chicks are 30 days old, when there is a transition of Scare Off Chicks. Females stay in this state until the chicks are 18 days old, when they either make a transition to Start a New Brood, or if this is their fourth breeding attempt will wait until the chicks are 30 days old and then do Stopping Breeding.

Egg Hatch - Female
A transition is made to Care for Young, and a message is sent to the male to do the same.

Incubation
Incubation occurs as described in development above. The female spends that time off the nest required to find energy to cover her basal metabolic requirements, plus that energy required to warm the eggs. Incubation continues until the eggs hatch and there is a transition to Care For Young, or the incubation period (MID) is exceeded, at which point the female will Start New Brood.

Egg Laying
The female produces one egg per day, if she has built up sufficient energy reserves to acomplish this.

Stopping Breeding
The female gives up the territory for this year, informs here mate, and makes a transition to Flocking.

Building up Resources

The female forages from her home range each day. The food resources she collects are reduced by her existence metabolism, the remaining is then converted to stored energy. When this energy exceeds ECEL, she will make a transition to Make Nest.

Make Nest
When weather conditions are better than TTB the female begins construction of a nest in the best nesting habitat in her territory. Construction takes NB days, after which there is a transition to Egg Laying. Energetic resources are continually built up during this period (see Building Up Resources).

Give Up Territory
The female gives up the territory for this year, informs here mate, and makes a transition to Floating.

Start New Brood
The female assesses the habitat quality of the territory. If still suitable (i.e. above MTQ) she will make a transition to Make Nest, otherwise she will go to Give Up Territory.

Name	**Description**	Value	**References**
AEW	Average egg weight	3.25g	Own data (N=1259)
ECR	Egg cooling rate	b = 6.204 $w^{-0.3965}$ ± 1.080] = 2.9 °C Time $^{-1}$ °C $^{-1}$ w = egg weight in g	[2]
IT	Incubation temperature	35.0 ° C	[2]
DI	Duration of incubation	88 day °C above 26°C	Own data (N=363); [3]
MID	Max. incubation duration	14 days	Own data
TDE	Threshold for physiological development of eggs	26 °C	[3]
MGR	Max. growth rate of nestlings (1-8 days)	3.75g day^{-1}	Own data (N=496)
FF	Max. feeding frequency/nest /day during the nesting period	45	[4]
TTB	Threshold temperature for initiation of breeding	Mean daily temp. >10°C	[5]
JI	Juvenile independence	30 days from hatching	[5]
NB	Duration of nest building: 1st attempt; successive attempts; after loss of nest	1st (3 days), successive (4 days), after loss (5-6 days)	[5, 6]
CLS	Clutch size in relation to nest attempt (1– 4)	[1st att.: 2 (6%), 3 (23%). 4 (62%), 5 (9%)] [2. att.: 3 (32%), 4 (64%), 5 (13%)] [3 att. : 3 (16%), 4 (74%), 5 (10%)] [4 att. : 4 (29%), 5 (71%)]	Based on own data (N=363)
WID	"Windy day" (mean wind speed) for nestlings	4 m sec^{-1}	Estimate
WD	"Wet day" (mean daily precipitation) for nestlings and parental foraging	5.5 mm	Estimate
CD	"Cold day" (mean daily temperature) for nestlings	9°C	Estimate
MPF	Max. Precipitation for parental feeding (daily mean)	20 mm	Estimate
ECI	Energy cost of incubation	An standard value of 2.4 kcal clutch -day^{-1} is used	[2]
ECEL	Energy cost of egg laying	Calculated from: q = 1.124 $w^{-0.9438}$ ± 1.088 kcal egg^{-1} = 4.44 kcal, and: M = (q x n)/0.77 (n + d) kcal (clutch)	[2]
IA	Insect assimilation constant	= 0.74	[7]
EMJ	Existence metabolism for juveniles (age 1-40)	M = 0.518614 x $W^{1.1263}$ kcal bird $^{-1}$ day $^{-1}$	[2]

		Calculated from own data, adjusted for skylark weight (W)	
EMA	Existence metabolism for Adults	31.2 – 0.440T kcal bird $^{-1}$ day $^{-1}$ T = ambient temperature	[2]
CE	Age-specific conversion efficiency of g dry-weight insects to body weight (age:1-30 days)	CE = 1.180 – 0.035742 x age	[2]
NW	Nestling weight at nest leaving	21g (mean weight on leaving nest)	Based on own data (N=798)
AWM	Average weight for adult males	40.4g	Based on own data (29 individuals)
AWF	Average weight for adult females	36.4g	Based on own data (36 individuals)
ER	Extraction rate of arthropod food items	0.019	Fitting parameter
JM	Juvenile mortality; from independence until second year of life	35%	[5]
MIMM	Minimum yearly mortality for adult males (migration – over-wintering)	11%	[8]
MAMM	Maximum yearly mortality for adult males (migration – over-wintering)	50%	[9]
MIMF	Minimum yearly mortality for adult females (migration – over-wintering)	29%	[8]
MAMF	Maximum yearly mortality for adult females (migration – over-wintering)	71%	[9]
PFM	Pre-fledging mortality, juvenile mortality between nest leaving (day 7-11) and independence	1% day^{-1}	[5]
CMP	Clutch predation mortality (whole clutch)	1.4% day^{-1}	Own data
(N=363)			
NMP	Nestling predation mortality (whole brood)	2.5% day^{-1}	Own data
(N=238)			
MA	First male arrival in breeding area	From 14 January	Own data
FA	First female arrival in breeding area	From 1 February	[9, 5]
HRS	Home range size (diameter)	Maximum 280 m (from radio-tracked birds)	[1]
TD	Territory density (min. – max.)	0 – 100/100 ha	[8, 10, 5]
VQ	Vegetation quality, based on female nesting acceptability scores in relation to vegetation height (0-93cm, in 3cm divisions)	0, 100, 98, 86, 74, 65, 56, 48, 41, 35, 29, 25, 21, 18, 15, 13, 11, 10, 9, 8, 8, 8, 8, 8, 8, 8, 7 , 7 ,6 , 6 , 4	Modified from [11]
VH	Vegetation hindrance - hindrance to ground locomotion (combination of vegetation height and density) Biomass (g dry weight/m²)	Ht (cm) -300 -600 -900 -1200 0-25 0.00 0.10 0.20 0.30 26-50 0.05 0.25 0.60 0.80 51-75 0.33 0.65 0.85 0.93 75-100 0.55 0.70 0.90 0.95	[11,12]
MTQ	Minimum territory quality for female acceptance	144000	Fitting parameter

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