

**Pareto Front Analysis of Flight Time and Energy-Use
In Long-Distance Bird Migration**

Jasper A. Vrugt^{1*}, Jelmer van Belle², and Willem Bouten²

*Corresponding author. Email: vrugt@lanl.gov – Fax: 505-665-8737 – Phone: 505-667-0404

¹Jasper A. Vrugt, Earth and Environmental Sciences Division, Los Alamos National Laboratory, Mail Stop T003, Los Alamos, NM 87545

²Jelmer van Belle and Willem Bouten, Faculty of Sciences, Computational Bio- and Physical Geography, University of Amsterdam, Nieuwe Achtergracht 166, 1018 WV Amsterdam, The Netherlands

Jelmer van Belle: jvbelle@science.uva.nl

Willem Bouten: wbouten@science.uva.nl

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1 **ABSTRACT**

2

3 Optimality models are frequently used in studies of long distance bird migration to help
4 understand and predict migration routes, stopover strategies and fuelling behaviour in a
5 spatially varying environment. These models typically evaluate bird behaviour by
6 focusing on a single optimization currency, such as total migration time or energy-use,
7 without explicitly considering trade-offs between the involved objectives. In this paper,
8 we demonstrate that this classic single-objective approach downplays the importance of
9 variability in bird behaviour. In the light of these considerations, we therefore propose to
10 use a full multi-criteria optimization method to isolate the set of non-dominated, efficient
11 or Pareto optimal solutions. Unlike single-objective optimization where there is only one
12 combination of bird behaviour maximizing fitness, the Pareto solution set represents a
13 range of optimal solutions to conflicting objectives. Our results demonstrate that this
14 multi-objective approach provides important new ways of analyzing how environmental
15 factors and behavioural constraints have driven the evolution of migratory behaviour.

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1 **1. Introduction and Scope**

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3 One of the central goals in avian biology is to understand the behavioural strategies that
4 birds adopt in real-world environments. Faced with the complexity and variability in
5 nature, and the difficulty of performing controlled experiments, a variety of theoretical
6 optimization models have been developed to help understand and examine migratory
7 behaviour of birds. These models range from simple mathematical equations predicting
8 the stopover duration at a given site when optimizing energy or time (Alerstam and
9 Lindström 1990; Hedenström and Alerstam 1997; Weber and Houston 1997a; Houston
10 1998) to spatially explicit individual-based models in which birds migrate over a
11 simulated environment given a set of behavioural rules (Erni et al. 2002, 2003).
12 Irrespective of the dimensionality and complexity of these models, it is assumed that the
13 bird's behaviour can be understood and predicted by posing the migration problem into
14 an optimality framework. In such a framework, the behavioural strategy of a bird is
15 evaluated against some prior defined fitness measure (e.g. time, energy and risk of
16 predation), given appropriate biological and environmental constraints. The behavioral
17 strategy that maximizes (as appropriate) this predefined fitness measure is then compared
18 with observed behaviour. The advantages of this optimality approach are not difficult to
19 enumerate: the fitness of any behavioural strategy, defined by a collection of decisions
20 and actions can be directly evaluated in terms of the bird's ability to reach the considered
21 objectives, and perhaps most importantly, the strengths of modelling and measuring bird
22 behaviour are combined in a natural way.

1 In the pioneering work by Alerstam & Lindström (1990) two main currencies
2 were developed that birds might seek to optimize during a migratory episode. Minimizing
3 energy cost of transport is one strategy that could be used by migrating birds, especially
4 short-distance migrants. An alternative currency is the time spent on migration, a
5 currency most likely to be important for long-distance migrants (Weber and Houston
6 1997). With some notable exceptions (Houston 1998) most optimality models used in
7 avian biology generally obtain predictions assuming either time or energy minimization,
8 without interpreting the range of adaptive compromises between these two conflicting
9 objectives. So, current optimality models do not place emphasis on interpreting
10 variability in behaviour that arises from differential weighting of flight time and energy-
11 use. Such an analysis would help understand the dominating selection factors that explain
12 the bird's behaviour in different situations. For instance, it would be useful to see if and
13 when migration is primarily time-selected, energy-selected and so on.

14 In this paper, we present a novel concept of multi-objective optimization that
15 proves very useful to interpret variability in the analysis of migration behaviour of birds.
16 This multi-objective method operates by defining several performance criteria (objective
17 functions) that reflect different (complementary) objectives of the animals' behaviour and
18 uses a full multi-criteria optimization method to identify the range of optimal solutions.
19 (Schmitz et al. 1998). These Pareto solutions represent tradeoffs among the different
20 incommensurable and often conflicting objectives, having the property that moving from
21 one solution to another, results in the improvement of one objective while causing
22 deterioration in one or more others. To illustrate the power and applicability of our
23 approach, we consider a two-dimensional spatially explicit individual based dynamic

1 state variable model simulating the long-distance migration of passerine birds. Objective
2 functions that will be considered are those that seek to minimize flight time (and thus
3 maximize the speed of migration), and minimize energy-use of transport (Alerstam and
4 Lindström 1990). The resulting optimization problem was solved using a MATLAB
5 implementation of the Multi-Objective Shuffled Complex Evolution (MOSCEM-UA)
6 global optimization algorithm (Vrugt et al. 2003a).

7 This paper is organized as follows. Section 2 presents a condensed description of
8 the basic optimality approach and describes the classical single objective optimization
9 methods used to study animal behaviour. In Section 3 we provide a carefully built
10 demonstration of the limitations of single-objective methods by application to the long-
11 distance migration of passerine birds using a two-dimensional spatially explicit
12 simulation model. In Section 4 we subsequently discuss the rationale and architecture of
13 our multi-objective approach, and pose the bird migration problem into a multi-objective
14 optimization framework. The resulting inverse problem is solved using the computerized
15 MOSCEM-UA algorithm. Finally, in section 5 we summarize the results.

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17 **2. Optimization of bird migration**

18 **2.1. Basic Inverse Problem**

19

20 The fundamental problem with which we are concerned is to predict the behavioural
21 strategy of a bird that maximizes some predefined objective given appropriate biological
22 and environmental constraints. The formulation of this resulting optimization problem can

1 be expressed in a generic form if we weight the n fitness functions, $f_i(\theta)$ into one
2 aggregated scalar, $F(\theta)$:

3

$$4 \quad \min_{\theta} F(\theta) = w_1 \cdot f_1(\theta) + \dots + w_n \cdot f_n(\theta) \quad (1a)$$

5

6 subject to:

7

$$8 \quad h_i(\theta) = b_i \quad \text{for } i = 1, \dots, k \quad (1b)$$

9

10 where θ is a parameter set, which defines the behavioural strategy of the animal, w_i
11 denotes a particular weight, and $h_i(\theta)$ and b_i represent k anatomical or physiological
12 constraints on behaviour or life-history (Schmitz et al. 1998).

13

14 **2.2. Single objective optimization**

15

16 Current optimality models used in avian migration typically use time and energy as main
17 criteria in Eq. (1), using values for the weights of 1/0 and 0/1 to result in pure time or
18 energy minimization, respectively. The solution to this optimization problem is by its
19 very nature a single optimal strategy. However, in real-world environments animals often
20 do not match any single predicted optimum exactly, but instead exhibit broad variation in
21 performance (Ward 1992; Schmitz et al. 1998; Rothley 2002). Using a single set of
22 weights in the optimality analysis effectively neglects complex optimal solutions arising

1 from differential weighting of the various involved currencies, and therefore downplays
2 variability in migratory behaviour.

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4 **3. Application of single-objective optimization to long-distance bird migration**

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6 To illustrate the limitations of the single-objective approach set forth in Eq. (1) we
7 consider the autumn migration of Willow Warblers over Continental Europa and northern
8 Africa using a two-dimensional spatially explicit individual based simulation model. In
9 this section we first describe the bird migration model used to conduct our analysis, and
10 then discuss the limitations of conventional optimization.

11

12 **3.1. Case study**

13 **3.1.1. Spatially explicit modelling framework**

14

15 We developed a two-dimensional spatially explicit dynamic model that simulates the
16 time evolution of the spatial location and airframe, muscle, and fat amounts of an
17 individual bird under a given set of behavioural rules. These rules, being characterized by
18 a set of parameter values, define the decisions and actions of the bird that experiences
19 dynamic environmental conditions. The model combines the strengths of the flight
20 mechanical theory presented in Pennycuick (1998; 2003) and the two-dimensional
21 spatially explicit modelling framework of Erni et al. (2002; 2003), but includes several
22 additional features to increase flexibility and applicability. In this section we describe the
23 most important components of the model.

1 The environment is discretized into a two-dimensional rectangular equidistant
2 grid of cells ranging from -20 by 40 degrees longitude to 10 by 70 degrees latitude using
3 a grid resolution of 0.5° in both directions. This results in a structured mesh of 120 by
4 120 cells. Each spatial cell was assigned a different Fuel Deposition Rate (FDR) based on
5 work reported in Hedenström and Alerstam (1997), Weber (1999) and Erni et al. (2002;
6 2003). The meteorological conditions (wind direction and speed) at each spatial cell are
7 hourly updated using linear interpolation between two consecutive 6-hourly predicted
8 wind maps from reanalysis runs of the NCEP model of the National Oceanic and
9 Atmospheric Administration (NOAA). These data can be obtained from the following
10 website: <http://www.cdc.noaa.gov/cdc/data.ncep.reanalysis.html>.

11 The simulations are calculated with time intervals of 1 hour and starts at August
12 1, 2004 to consider autumn migration. A condensed flow diagram of the dynamic part of
13 the model appears in Figure 1. The timing of flight and stopover is characterized by a
14 flight cycle, consisting of a preset number of flight and rest days (indicated with N_{fly} and
15 N_{rest} respectively). As we consider nocturnal migrants, birds intent to fly during the period
16 between evening and morning civil twilight. The exact start and length of this period is
17 computed at each day and spatial location in the considered grid domain. The final
18 decision to take-off or to keep flying depends on the fat reserves and the experienced
19 wind conditions at the 850 mbar level (Liechti and Bruderer 1998; Schaub et al. 2004). If
20 the fat reserves or net speed of the bird drop below two user-defined thresholds (named
21 m_{minfat} and V_{min}) the bird will not take-off or in the case of active flight, will stop flying.
22 When not in flight, the birds rest or refuel depending on the search and settling time
23 (Klaassen and Biebach 1994). Refuelling rate is computed as the net effect of the

1 experienced FDR at the stopover site and the basal metabolic rate (BMR), which process
2 also continues during non-flight hours. The BMR was calculated using the work by
3 Lasiewski and Dawson (1967) for passerine birds.

4 During active flight, the speed of the bird including its associated mechanical
5 power and energy equivalent are computed using the flight mechanical framework of
6 Pennycuick (1998) given a preset speed option (maximum range, minimum power or
7 constant speed). Variables needed in this computation, and the values assigned to them,
8 are listed in Table 1. Heading, net speed and direction are subsequently calculated using
9 the current experienced wind conditions in the respective cell in combination with the
10 preferred direction and a wind compensation or drift factor (Alerstam and Pettersson
11 1977; Alerstam 1990; Liechti and Bruderer 1998). The wind compensation factor
12 (referred to as P_{wind} in the model) determines how much the bird is using of its own speed
13 to compensate for the wind vector (defined by wind direction and speed). No
14 compensation will result in complete wind drift, where the net direction becomes the
15 resultant of the wind vector and bird vector. A full compensation means that the bird is
16 utilizing its flight speed to compensate for the wind vector by adjusting its heading, so its
17 net (resultant) direction becomes as close as possible to the preferred migration direction.

18 The preferred direction is based on the endogenous direction and on large-scale
19 geography: coastlines, barriers and borders of barriers affect the preferential direction, in
20 a similar way as implemented by Erni et al. (2002; 2003). Passerines avoid flying over
21 large water bodies and if they do, they will cross perpendicular to the coastline.
22 Information about large-scale topography, water bodies, and FDR are included in a
23 landscape map. Depending on the chosen protein burn criteria (specific work held

1 constant, power density held constant, or muscle mass held constant) the energy used
2 during flight is distributed between airframe, muscle and fat consumption (see
3 Pennycuick 1998). At the end of the hourly calculation interval, the new position of the
4 bird in the spatial domain, the cross-sectional area of the body, wingbeat frequency, and
5 the remaining mass of fat, airframe and muscle are updated. This time-marching
6 computation continues until the bird either covers the required distance to complete the
7 journey, or runs out of consumable fat reserves, or when the simulation time exceeds 200
8 days.

9

10 **3.1.2. Speed calculation, muscle burn criteria and target destination**

11

12 At each hourly calculation interval the speed of the bird is computed as a constant factor
13 (1.2; see Table 1) of the minimum power speed (V_{mp}) (Pennycuick, 1998). Moreover, the
14 hypothesis underlying all our calculations is that no muscle tissue is consumed and that
15 no energy is derived from oxidizing protein (e.g. Jenni and Jenni-Eiermann 1998;
16 Pennycuick 1998). Although various investigations have demonstrated that both these
17 assumptions can be contested, they avoid a problem which becomes apparent during a
18 refuelling phase. If protein is used as energy source, not only the fat reserves would
19 decline during a long migratory flight, but also the muscle and airframe mass. During
20 refuelling phases, it would then need to be made explicit how birds distribute their energy
21 intake to build up their airframe, muscle and fat mass again. As not much is known about
22 this distribution function and its spatial and temporal variation, we decided to use the
23 constant muscle mass option with no protein burn.

1 As the orientation and navigation behaviour of passerine birds is still subject of
2 ongoing debate with not much consensus (e.g. Mouritsen 1998; Wiltschko et al. 2001;
3 Thorup and Rabøl 2001) we decided to implement a quite simplistic set of rules: the
4 orientation and target direction are assumed perfectly known during the entire migration.
5 The target direction of the bird during autumn migration is computed during the
6 initialization of the model from the geographical location of the breeding ground and
7 endogenous direction ($Dendog_{fall}$) using an arrival location at 15° north latitude.

8

9 **3.1.3. Model parameters subject to optimization**

10

11 Table 2 provides a detailed overview and description of the most important parameters in
12 the bird migration model. A distinction is made between default values and parameters
13 subject to optimization. As this illustrative case study considers the migration of the
14 Willow Warbler, the default values correspond to those given in the literature by
15 Hedenström and Pettersson (1984; 1987) for this nocturnal migration. For the other
16 (calibration) parameters upper and lower bounds are specified, together defining the
17 feasible space of behavioural rules. Note that some fuzziness exists in the selection of the
18 calibration parameters. The decision to select this set of calibration parameters was based
19 on arguments of maximum variation in behavioural rules with the lowest possible number
20 of adjustable parameters.

21 Most of the parameters that appear in Table 2 have been previously discussed in
22 the description of the model in section 3.1 of this paper. We therefore limit ourselves to
23 those parameters that have not been given sufficient discussion. The parameter $initfat_{fall}$

1 defines the fat mass at the start of the autumn migratory journey. Tuning this parameter
2 provide a useful way to explore the influence of the initial conditions on the “optimal”
3 migration route, given variations in the environmental conditions and behavioural rules.
4 In addition, $m_{crossfat}$ signifies the minimum fat reserve of a bird needed to be able to
5 successfully cross the desert and arrive at its wintering grounds. Only when the fat
6 reserve is larger than this user-defined threshold, the bird will decide to cross the desert.
7 Otherwise, the bird will remain at its stopover site and wait for his fat mass to build up to
8 the level of $m_{crossfat}$. When this condition is satisfied the bird will decide to take-off at
9 evening civil twilight, if the net speed is larger than V_{min} . Other approaches in the
10 literature consider a user-defined fat threshold that depends on the extent of the desert
11 barrier, to signify the minimum amount of fuel for a bird to cross the desert. In the
12 absence of prior information on the size of this fat threshold, we decided not to
13 incorporate this approach, but instead to give the bird maximum flexibility in choosing its
14 migration strategy by optimizing $m_{crossfat}$.

15

16 **3.1.4. Selection of objective functions**

17

18 To implement the single-objective optimization procedure outlined in section 2 of this
19 paper, it is necessary to specify a set of relatively unrelated objectives, $f_i(\theta)$, that measure
20 different but complementary parts of bird behaviour. Most optimality models that have
21 been developed in the ecological literature only consider flight time to be the main
22 objective (Alerstam and Lindström 1990; Weber et al. 1998; Weber and Houston 1997;
23 Hedenström and Alerstam 1997). It has, however, been frequently hypothesized that birds

1 not only tend to minimize flight time, but simultaneously also seek to minimize energy-
2 use and maximize safety (Alerstam and Lindström 1990; Houston 1998; Weber et al.
3 1998; among others).

4 In the context of bird migration, it is particularly difficult to formalize a
5 mathematical framework that defines safety under a changing set of environmental
6 conditions and behavioural rules (e.g. Lank and Ydenberg 2003; Lind 2004). In this case
7 study, we shall therefore employ a rather simple optimization hypothesis: birds are trying
8 to minimize migration time (measured by f_T) and energy-use (measured by f_E) during
9 their autumn migratory journey using adaptive compromises to this trade-off problem.
10 Migration time is being defined as the number of days needed to complete the autumn
11 migration (days), while energy-use refers to the daily average energy consumption (kJ
12 day⁻¹) during this journey. This f_E currency is computed as the ratio between the total
13 energy-use during periods of flight (chemical power) and stopover/refuelling (basal
14 metabolic rate) to f_T .

15

16 **3.2. Results of classical single-objective optimization**

17

18 Figure 2 depicts the migratory pathways corresponding to three independent single-
19 objective optimization runs using different weights for the f_T (1) and f_E (2) objectives and
20 a starting location of the Willow Warbler in south-western (60.0° N, 10.0° W)
21 Scandinavia. The first two runs minimize migration time (solid line; $w_1 = 1$; $w_2 = 0$) and
22 daily energy-use (dashed line; $w_1 = 0$; $w_2 = 1$) respectively, whereas the third run weights
23 the two criteria equally to obtain a single aggregated fitness measure (dotted line; $w_{1,2} =$

1 0.5). In addition, Table 3 lists the corresponding parameter estimates obtained using a
2 Parallel Computing implementation of the Shuffled Complex Evolution (SCE-UA) global
3 optimization algorithm (Duan et al. 1993).

4 The results presented in Figure 2 and Table 3 demonstrate that the optimal
5 migration direction of the Willow Warbler heavily depends on how the bird seeks to
6 compromise between flight time and energy-use. The depicted variation in behaviour
7 represents a range of adaptive compromises to total migration time, and energy cost of
8 transport. Unfortunately, it remains unclear which differential weighting is associated
9 with the highest fitness as all three migration strategies result in a successful arrival at the
10 wintering ground, and thus represent equally efficient (adaptive) compromises to the
11 trade-off problem.

12 In principle it would be possible to say how much weight should be given to
13 conflicting objectives if lifetime success is to be maximized. For example, in the case of
14 bird migration, by considering a single migratory journey in the context of the bird's life
15 history it is possible to specify what the terminal reward at the end of a migratory journey
16 should be (McNamara et al. 1998). However, it would be desirable to have an
17 optimization strategy that provides the entire range of adaptive solutions to conflicting
18 objectives. Such a method would provide important insights and help understand how the
19 individual objectives, influence the common currency or lifetime reproductive success.
20 Also a single common currency will bias variation in animal performance and downplay
21 variability. Moreover, it is difficult to mathematically develop a single common currency,
22 which is insensitive to the magnitude and units of the separate criteria.

1 In the light of these considerations, we therefore propose to implement a multi-
2 criteria analysis to define the set of efficient choices animals may make in attempting to
3 reach compromises among the various, often conflicting, criteria. There is arguably a
4 significant advantage to maintaining the independence of the various criteria, because a
5 multi-criteria optimization will allow an analysis of the tradeoffs among the different
6 criteria and enable avian biologists to better understand the meaning of variability in
7 migration behaviour of birds. An important feature of this approach is that, within the set
8 of alternatives, no choice can be considered *a-priori* to yield higher fitness than any other
9 choice. In the next section we demonstrate that considerable insights into the abilities of
10 animals to make optimal decisions can be gained by analyzing this set of efficient
11 choices.

12

13 **4. Towards improved modelling of animal behaviour**

14 **4.1 Multi-objective optimization**

15

16 The propositions set forth in the previous section imply the design of an optimization
17 strategy that has the ability to simultaneously incorporate several objective functions. A
18 strategy that can address this challenge is multi-objective optimization and can be stated
19 as follows:

20

21
$$\min_{\theta \in \Theta} F(\theta) = \begin{bmatrix} f_1(\theta) \\ \vdots \\ f_n(\theta) \end{bmatrix} \quad (3)$$

22

1 where $f_i(\theta)$ is the i^{th} of the n objective functions. The solution to this problem will in
2 general, no longer be a single “best” parameter set but will consist of a Pareto set $P(\Theta)$ of
3 solutions in the feasible parameter space Θ corresponding to various trade-offs among the
4 objectives. The Pareto set of solutions defines the minimum uncertainty (variability) that
5 can be achieved without stating a subjective relative preference for maximizing one
6 specific component of $F(\theta)$ at the expense of another. To illustrate this concept, consider
7 Figure 3 which depicts the Pareto solution set for a simple problem where the aim is to
8 simultaneously optimize two objectives (f_1, f_2) with respect to two parameters (θ_1, θ_2) . The
9 individual points A and B optimize objectives f_1 and f_2 , respectively, whereas the solid
10 line joining A and B represents the theoretical Pareto set of solutions. The black dots
11 indicate an initial set of parameter estimates, while the number in subscript denotes their
12 corresponding Pareto rank. Moving from A to B along the line results in the improvement
13 of f_2 while successively causing deterioration in f_1 . The points falling on the line AB
14 represent trade-offs between the objectives and are called non-dominated, non-inferior, or
15 efficient solutions. Put simply, the feasible parameter space can be partitioned into
16 “good” or Pareto solutions and “bad” or “inferior” solutions. In the absence of additional
17 information, it is impossible to distinguish any of the Pareto solutions (rank 1 points) as
18 being objectively better than any of the other Pareto solutions. Because of conflicting
19 demands, it is usually not possible to find a single point θ at which all of the criteria have
20 their minima.

21

22

23

1 4.2. Pareto solution algorithms

2
3 While it may be relatively simple to pose the bird migration problem into a multi-criteria
4 framework, solving this problem to identify the Pareto set of solutions is not easy and has
5 been the subject of much research. Ideally, the multi-objective optimization algorithm
6 should find the set of all non-dominated solutions, which will constitute the global trade-
7 off surface. However, because computational resources are finite, multi-objective
8 solution algorithms typically approximate the Pareto set using a number of representative
9 solutions.

10 For linear models, multi-objective linear programming (MOP) methods can be
11 used to analytically derive the set of efficient or non-dominated Pareto solutions (Cohon
12 1978). However, for nonlinear settings with a dynamic state variable model, such as the
13 spatially explicit bird migration model considered in this paper, an alternative class of
14 solution algorithms is needed. Fortunately, the field of optimization theory has studied
15 the multi-objective optimization problem for dynamic nonlinear state models quite
16 extensively (Giocoechea et al. 1982). These methods for obtaining Pareto solutions can
17 be categorized as a posteriori methods, a priori methods, and interactive methods.
18 Presentations and discussions of these methods can be found in textbooks (Giocoechea et
19 al. 1982; Szidarovsky et al. 1986) and in review papers (Hipel 1982; Szidarovsky and
20 Szenteleki 1987; Yapo et al. 1992).

21 The overriding characteristic of classical multi-objective optimization methods is
22 the sequential generation of the Pareto solutions. As an illustration, consider the
23 weighting method of Eq. (1) in which each objective is allocated a weight, and the multi-

1 objective problem is converted to a single-objective problem. This problem can be easily
2 solved using classical optimization methods, as previously illustrated in section 3 for
3 three combinations of the weights. By randomly assigning different values for the
4 weights, we can generate as many discrete Pareto solutions as necessary to obtain an
5 acceptable approximation of the continuous Pareto space. However, this method is
6 computationally very demanding, as for each discrete Pareto solution a complete single-
7 objective optimization must be solved. This especially becomes problematic when an
8 increasing number of fitness measures are included in the multi-criteria analysis. Note
9 that conventional optimization approaches used in ecology could, in principle be
10 extended to a multi-criteria implementation when optimizing the terminal reward with
11 different weights for the criteria. However, as argued earlier, this aggregation approach is
12 computationally very expensive.

13 Fortunately, an efficient nonclassical method for solving the multi-objective
14 optimization problem in its original form has recently been developed by Vrugt et al.
15 (2003a). The method, entitled the Multi-Objective Shuffled Complex Evolution
16 Metropolis (MOSCEM-UA) algorithm, is a general purpose global optimization method
17 that provides an efficient estimate of the Pareto solution space within a single
18 optimization run and does not require subjective weighting of the various objectives. The
19 MOSCEM-UA algorithm combines the strengths of the complex shuffling employed in
20 the SCE-UA algorithm (Duan et al. 1993), the probabilistic Metropolis-annealing search
21 procedure (Metropolis et al. 1953) of the SCEM-UA algorithm (Vrugt et al. 2003b) and
22 an improved version of the fitness assignment concept of Zitzler and Thiele (1999) to
23 construct an efficient and uniform estimate of the Pareto solution set. A detailed

1 description and explanation of the method are given in Vrugt et al. (2003a) and so will
2 not be repeated here.

3

4 **4.3. Application of multi-objective optimization to bird migration modeling**

5

6 A Parallel Computing implementation of the MOSCEM-UA algorithm was used to
7 estimate the Pareto optimal solution space for the two measures f_T and f_E . The procedure
8 used 10,000 model evaluations to converge to an estimate of the Pareto set. The results of
9 this two-criteria $\{f_T, f_E\}$ optimization are summarized in Figures 4 and 5 and discussed
10 below.

11 Figure 4 presents normalized parameter plots for each of the parameters of the
12 bird migration model using the MOSCEM-UA algorithm. The model parameters are
13 listed along the x -axis, while the y -axis corresponds to the parameter values scaled
14 according to their prior uncertainty ranges (defined in Table 2) to yield normalized
15 ranges. Each line across the graph represents one parameter combination and is
16 associated with a different combination of weights for flight time and energy-use. The
17 solid and dashed black lines going from left to right across the plots correspond to the
18 best single objective solutions of f_T and f_E , previously discussed in section 3.2, while the
19 grey lines denote members of the Pareto set of solutions. The $\{f_T, f_E\}$ objective function
20 plots on the right-hand side in Fig. 4 depict two-dimensional projections of the bi-
21 criterion trade-off surfaces represented by the Pareto set of solutions.

22 The results presented in Fig. 4 emphasize several important observations. In the
23 first place, notice that the Pareto trade-off region remains of considerable size, when

1 compared to the initial parameter uncertainty. For most of the parameters the Pareto
2 solution space occupies a significant part of the predefined feasible space of actions and
3 decisions, suggesting that birds have quite some flexibility in choosing an “optimal”
4 migration strategy. So, when considering the $\{f_T, f_E\}$ objectives simultaneously the space
5 of behavioural strategies does not collapse to a single strategy, as would have been the
6 case when solving a single-objective problem (see section 3.2), but remains of finite size.
7 In the course of seeking compromises between flight time and energy-use, different birds
8 vary the weightings they place on both these objectives. These weightings represent
9 equally efficient compromises to the trade-off problem and result in Pareto optimal
10 behaviour. Any parameter set chosen from within this Pareto space is a good solution in
11 the sense that it provides a certain trade-off in the minimization of the $\{f_T, f_E\}$ objectives.
12 Any other parameter set, outside this region, is a bad solution in the sense that it will have
13 worse values for both objectives than any other point within the Pareto set. This is further
14 demonstrated in the $\{f_T, f_E\}$ objective function plots at the right-hand side, where a
15 significant trade-off is found between flight time and daily energy consumption. Birds
16 that seek to minimize flight time do this at the expense of consuming more energy per
17 day, and vice versa.

18 While our current objective functions do not incorporate any knowledge of field
19 observations or ringing recoveries, the Pareto solution space results in bird behaviour
20 which closely mimics observed behaviour: (1) the mean optimized fat fractions at autumn
21 departure ($init_{fallfat}$) of 0.27 (expressed to total body mass) closely match measured fuel
22 amounts of similar size passerine bird species at the onset of their migratory journey
23 (Alerstam and Lindstrom 1990), (2) the Pareto range of V_{min} between 3 and 10 m s⁻¹ is in

1 good agreement with experimental results from studies focusing on the influence of wind
2 and rain on departure intensity (Erni et al. 2002; Schaub et al. 2004), (3) the Pareto
3 average migration speed of approximately 90 km day^{-1} is in excellent agreement with
4 observed migration speeds of about 85 km day^{-1} established from extensive ringing
5 recoveries (Hedenström and Pettersson 1987), and (4) the Pareto average fuel amounts at
6 arrival at the breeding and wintering grounds of between 0.1 and 1.6 gram is in the order
7 of measured arrival fuel amounts for similar size passerine bird species (Smith and
8 Moore, 2003), indicating that our model predicted fat mass dynamics is reasonable.
9 These results are particularly excellent, in the light of our large initial parameter ranges
10 and the fact that no direct observations are included in our objective functions.

11 The second, perhaps most interesting, observation is that the Pareto solution set
12 exhibits significant bifurcations in the parameter space with several non-overlapping
13 strategies of “optimal” behaviour. This is most apparent for the endogenous direction
14 (Dendog) and suggests a co-existence of two main migratory pathways of the Willow
15 Warbler over continental Europe. This finding is in excellent correspondence with
16 observed flight routes of the Willow Warbler, established from extensive ringing
17 recoveries (Hedenström and Pettersson 1984; 1987, Alerstam 1996). To facilitate
18 graphical interpretation of the results in the remainder of this paper, we have assigned the
19 two different clusters of solutions in Fig. 4 a different grey tint. Depending on how the
20 bird seeks to compromise between flight time and daily energy-use, the bird chooses its
21 preferred flight direction and arrival destination. This is further demonstrated in Figure 5,
22 which compares the observed center of gravity of migration of the Willow Warbler (Fig.
23 5A) with simulated Pareto optimal flight route trajectories (Fig. 5B). Each mapped line

1 from the breeding to the wintering grounds represents the flight route of one Pareto
2 solution.

3 Birds that seek to minimize flight time (light grey lines) should take a south-
4 southeast oriented flight direction, with an endogenous direction between 145 and 160
5 degrees. On the contrary, for birds that seek to minimize daily energy-use (dark grey
6 lines) it is most productive to take a more westerly oriented flight path with an
7 endogenous direction ranging between 180 and 195 degrees. An almost perfect match
8 with observed flight route trajectories is found for some Pareto solutions with south-
9 westerly oriented migration direction to the wintering grounds. These directions
10 (indicated with dark grey) correspond with solutions in the bi-criteria trade-off surface
11 that emphasize to minimize daily energy-use consumption. These results suggest that
12 during autumn migration Willow Warblers tend to minimize daily energy-use.

13 The discontinuity in optimal behaviour, so evidently found in the Pareto
14 parameter space, is also partly observed in the $\{f_T, f_E\}$ trade-off surface at the right-hand
15 side. We posit that the spatial and temporal varying environmental conditions in the
16 spatially explicit model introduce a high-degree of non-convexity in the response surface.
17 This explanation is also supported by additional multi-criteria optimizations in which we
18 neglected the influence of wind conditions and topography on the flight direction of the
19 bird. The outcomes of these numerical experiments clearly support this conjecture: The
20 MOSCEM-UA algorithm experienced less difficulty to converge to a limiting Pareto
21 distribution, and the non-dominated solutions were more closely clustered in the
22 parameter space. This suggests that niche separation in life-behavioural strategies is

1 facilitated by spatial and temporal variations in environmental conditions, an observation
2 that deserves further investigation in future research.

3 All in all, we can conclude that the multi-criteria optimization approach has
4 offered valuable insights into bird behaviour with the surprising result that for fall
5 migration, minimizing rate of energy consumption rather than duration of migration is
6 most important for explaining the Willow warblers' routes and behaviour. Note, however
7 that the results presented in this paper correspond to the analysis of one specific season.
8 An optimization analysis of geographical migration patterns is not complete without
9 considering combined effects during both autumn and spring. In another paper, we
10 present a multi-criteria analysis of a complete migration cycle (Vrugt and Bouten, 2006).

11

12 **5. Summary and conclusions**

13

14 In recent years significant progress has been made in the application of optimality
15 frameworks to study long-distance migration behaviour of passerine birds. However,
16 these frameworks typically evaluate behavioural strategies against a single decision-
17 making objective, which might embody several fitness components using a weighting
18 procedure, but underestimates the natural variability that exists in animal performance. In
19 the light of these considerations, we have introduced a more elaborate analysis
20 framework, called multi-objective optimization, which allows us to better examine
21 decision-making in complex environments and interpret the meaning of variability. A
22 multi-objective approach defines the set of efficient choices animals may make in
23 attempting to reach compromises among multiple conflicting objectives. This set defines

1 the Pareto solution space in which it is not possible to objectively select a specific
2 behavioural strategy as being superior to any other strategy within this space. So, instead
3 of weighting the various objectives into one aggregate scalar, each of the fitness
4 components is considered to be non-commensurate and its own entity. The size and
5 properties of the Pareto solution set and the sizes and properties of the trade-off range are
6 characteristics which will help to understand and predict animal behaviour.

7 The power and applicability of the multi-criteria approach, was demonstrated by
8 application to a two-dimensional spatially explicit individual based dynamic state
9 variable model simulating the long-distance migration of Willow Warblers. Objective
10 functions that were considered in the analysis include those that seek to minimize flight
11 time and energy-use. The resulting optimization problem was posed in a multi-criteria
12 framework and solved using the MOSCEM-UA global optimization algorithm. Through
13 this case study we have shown that the multi-criteria optimization approach provides an
14 excellent means to test the relative important of time and energy for the evolution of
15 migratory behaviour, Moreover, it has provided the insight that variability does not imply
16 lack of optimality.

17 Our current multi-objective optimization framework has used flight time and
18 energy-use to analyse the migration behaviour of birds. Although these two criteria seem
19 to be the most important in bird migration, the MOSCEM-UA algorithm is flexible and
20 can simultaneously handle a much larger number of objectives. To facilitate this, and
21 provide an efficient solution of the Pareto set, we have recently further improved the
22 efficiency of the algorithm by implementing genetically adaptive multi-method search
23 (Vrugt and Robinson, 2006).

1 The bird migration model is written in MATLAB7.0 and can be obtained from the
2 first author upon request. Optimization algorithms used in this and our other work are
3 available in the MATLAB and C-language and can be downloaded from:
4 <http://www.science.uva.nl/ibed/cbpg/software/>.

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7
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Table 1. Variables used in Pennycuick's flight mechanical framework

Name	Unit	Value
Body drag coefficient	[-]	0.10
Induced power factor	[-]	1.20
Air density	[kg m ⁻³]	1.23
Acceleration due to gravity	[m s ⁻²]	9.81
Ratio air speed: minimum power speed at start	[-]	1.20
Fat energy density	[J kg ⁻¹]	3.90·10 ⁷
Dry protein energy density	[J kg ⁻¹]	1.83·10 ⁷
Ratio water lost: protein consumed	[-]	2.20
Chemical power conversion efficiency	[-]	0.23
Circulation and respiration factor	[-]	1.10
Density of muscle	[kg m ⁻³]	1060
Mitochondria inverse power density	[m ⁻³ W ⁻¹]	1.2·10 ⁻⁶

Table 2: Most important parameters in the bird migration model: distinction is made between default values and those subject to optimization

Parameter	Description	Unit	Value/Range
<i>Default values^a</i>			
m_{musc}	Flight muscle mass	[g]	1.19
m_{frame}	Airframe mass	[g]	5.81
b	Wing span	[m]	0.193
S	Wing area	[m ²]	0.007
m_{maxfat}	Maximum fat mass	[g]	6.3
N_{fly}	Number of consecutive fly days	[d]	3
N_{rest}	Number of consecutive rest days	[d]	8
<i>Calibration parameters^a</i>			
m_{minfat}	Minimum fat mass during flight	[g]	0.0 – 4.0
$m_{crossfat}$	Minimum fat mass to cross barrier	[g]	2.0 – 5.0
$Initfat_{fall}$	Fat mass at start autumn migration	[g]	0.0 – 6.3
$Dendog_{fall}$	Endogenous direction autumn	[°]	130.0 – 230.0
P_{wind}	Wind compensation factor	[-]	0.0 – 1.0
V_{min}	Minimum net speed to take-off	[m s ⁻¹]	0.0 – 10.0

^aValues and ranges are based on experiments with Willow Warblers reported in literature (Hedenström and Pettersson, 1984; 1987).

Table 3: Optimized parameter values corresponding to minimization of migration time (run 1), energy-use (run 2) and an equally weighted combination of the two (run 3).

Parameter	Unit	Run 1	Run 2	Run 3
m_{minfat}	[g]	0.5	0.9	0.5
$m_{crossfat}$	[g]	2.0	3.0	2.0
$Initfat_{fall}$	[g]	5.7	2.8	3.4
$Dendog_{fall}$	[°]	147.8	186.6	150.1
P_{wind}	[-]	0.2	0.4	0.3
V_{min}	[m s ⁻¹]	5.9	9.0	4.7

Figure Captions

- Figure 1. Schematic flow diagram of the dynamic part of the bird migration model.
- Figure 2. Model predicted flight route trajectories corresponding to minimization of time (solid), energy-use (dashed), and a equally weighted combination of the two (dotted). The location of the breeding ground is indicated with a dot. The map is a Mercator projection.
- Figure 3. Illustration of the concept of Pareto optimality for a problem having two parameters (θ_1, θ_2) and two criteria (f_1, f_2) , in the parameter (A) and objective (B) space. The points A and B indicate the solutions that optimize each of the individual criteria f_1 and f_2 . The thick line joining A and B corresponds to the Pareto set of solutions; γ is an element of the solution set, which is superior in the multi-criteria sense to any other point in Θ .

Figure 4. Normalized parameter plots for the parameters in the bird migration model using a two-criteria $\{f_T, f_E\}$ optimization with the MOSCEM-UA algorithm. Each line across the graph denotes a single parameter set, solid and dashed black lines are single criterion solutions of f_T and f_E , respectively, and grey = Pareto solution set. The single-objective solutions are identical to those reported in Table 3. The squared panels at the right-hand side denote two-dimensional projections of the objective space of the Pareto set of solutions.

Figure 5. (A) Schematic overview of the center of gravity of migration of a population of Willow Warblers with a breeding ground in southwestern (60.0° N, 10.0° W) Scandinavia. The arrows indicate the flight direction. This Mercator projection is reconstructed from ringing recoveries by Hedenström and Pettersson (1984; 1987); (B) Simulated flight route trajectories during autumn migration. Each line represents one Pareto solution. Different grey tints are used to distinguish between southwest and southeast oriented migration direction.

While $\text{CurrentTime} < \text{TotalSimulationTime}$

- (1). Compute evening and morning civil twilight at current location
 - (2). Update body of bird
 - (3). Find speed and energy use
- } similar to Pennycuick (1998)
- (4). Should bird fly? (dependent on time, fly cycle and fat reserves)
 - Yes*
 - a) Load field with spatially variable wind conditions
 - (b) Compute net speed and direction using wind conditions
 - (c) Is net speed larger than user-defined parameter?
If *yes* bird takes-off, if *no*, bird will stay at stopover site
 - No*
 - (a) Bird will remain at stopover site
 - (5). Calculate new position
 - (6). Update airframe, muscle and fat amounts

$\text{CurrentTime} = \text{CurrentTime} + \Delta t$

Figure 1.

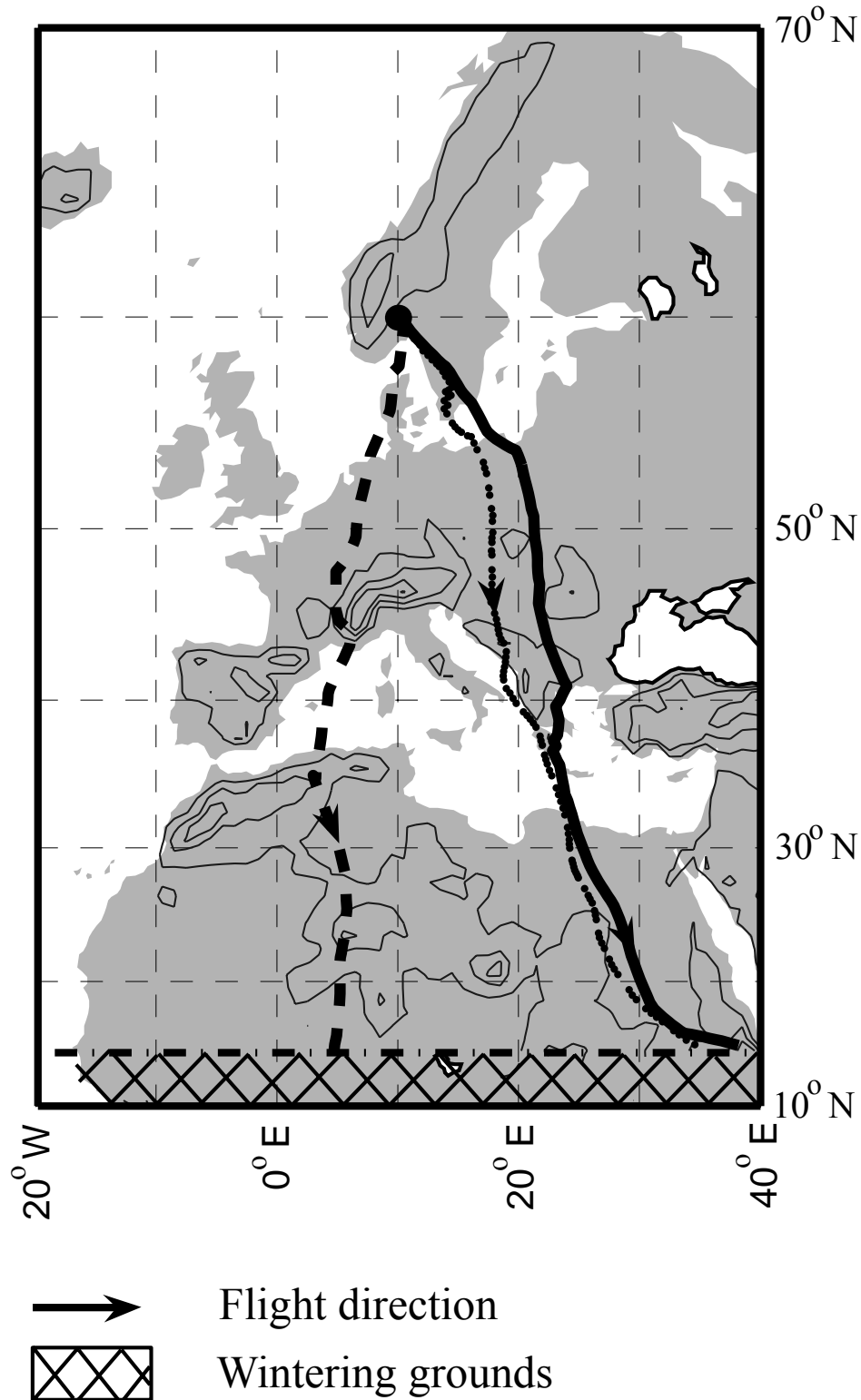


Figure 2.

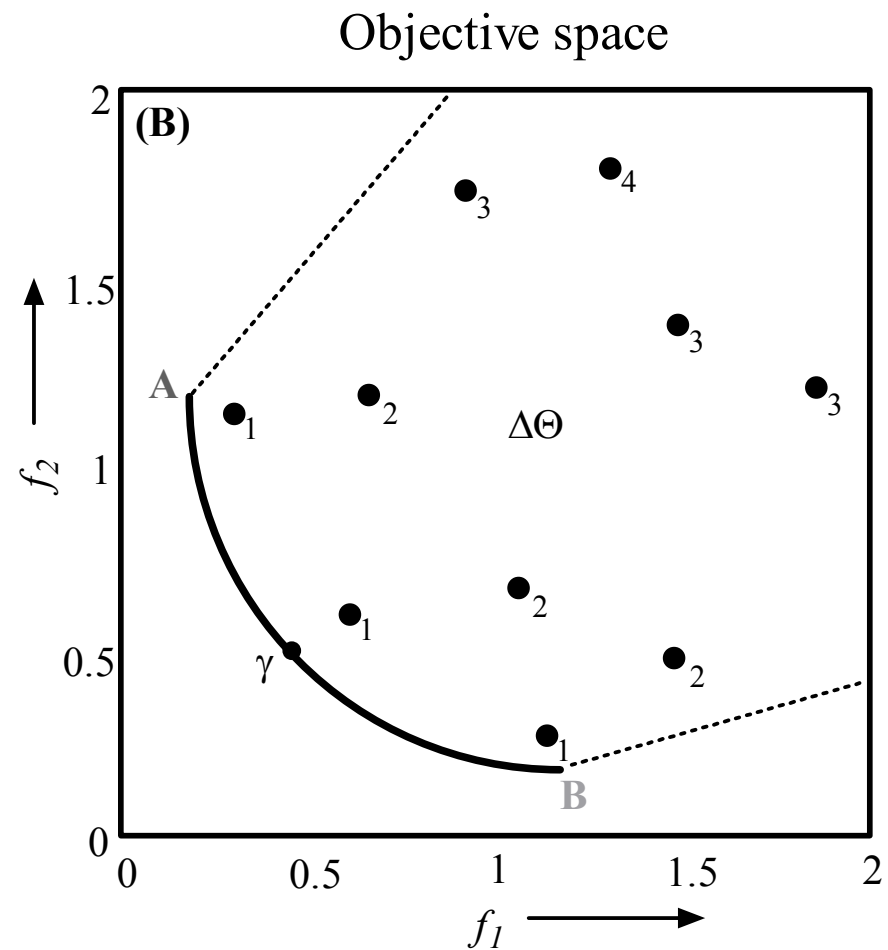
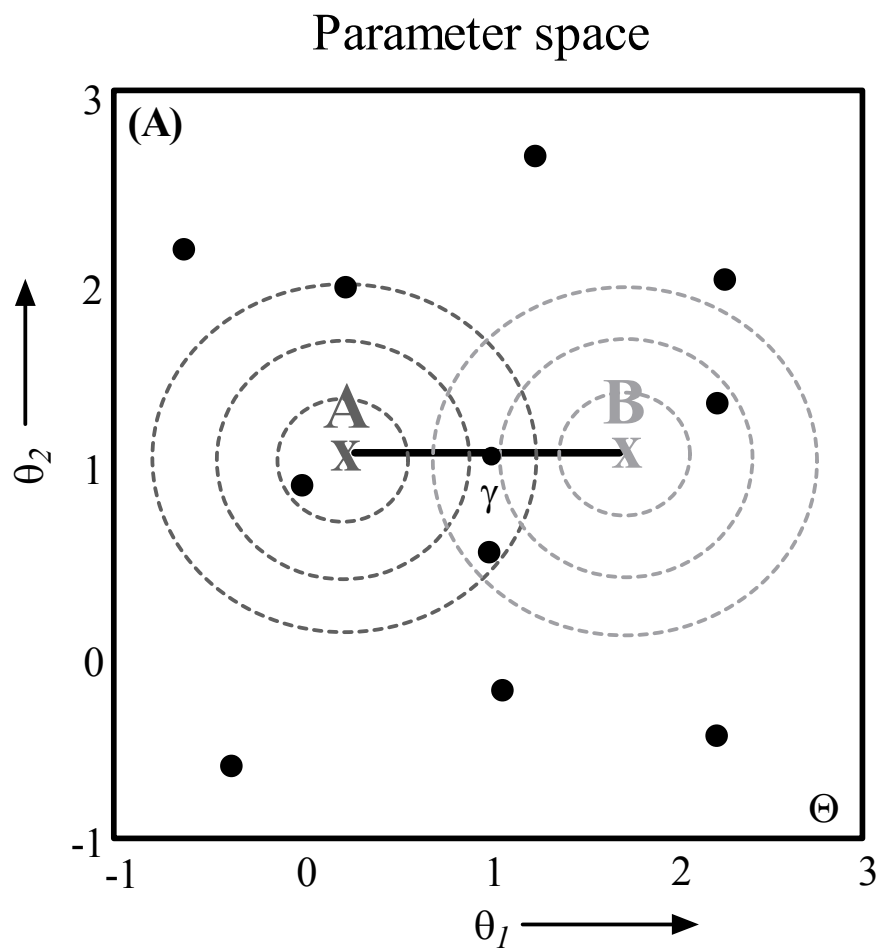


Figure 3.

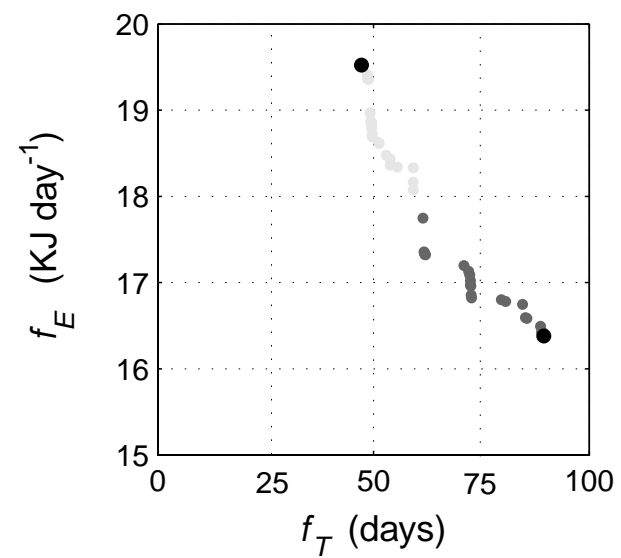
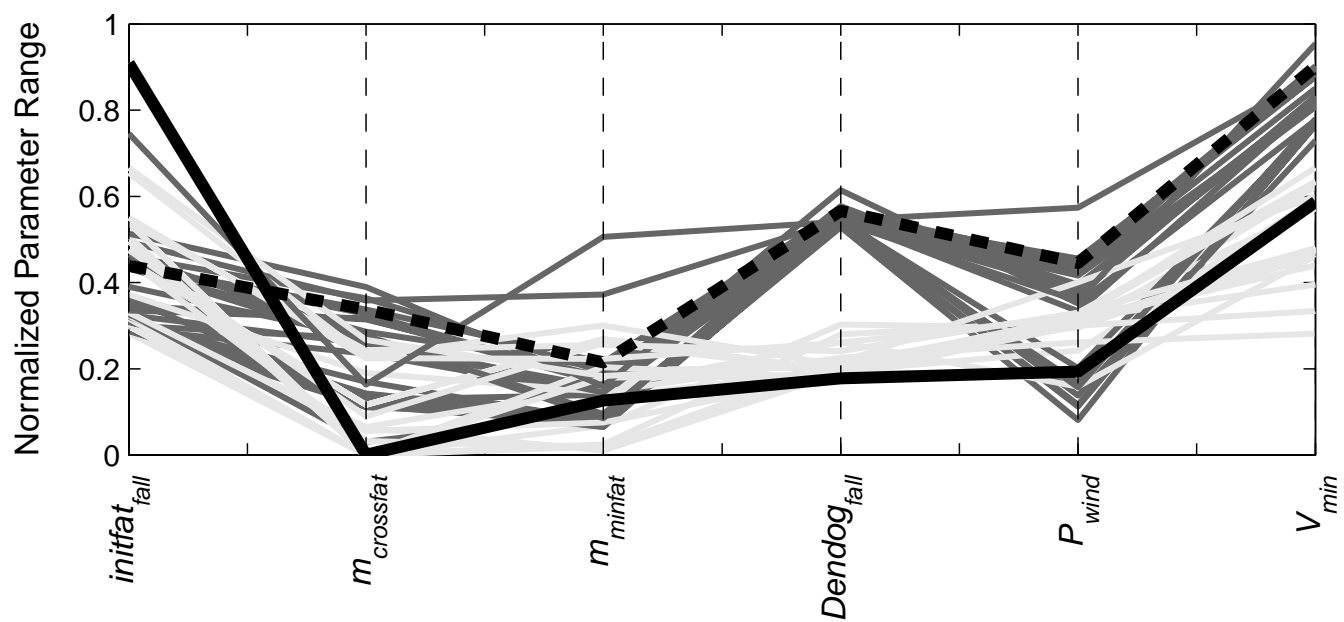
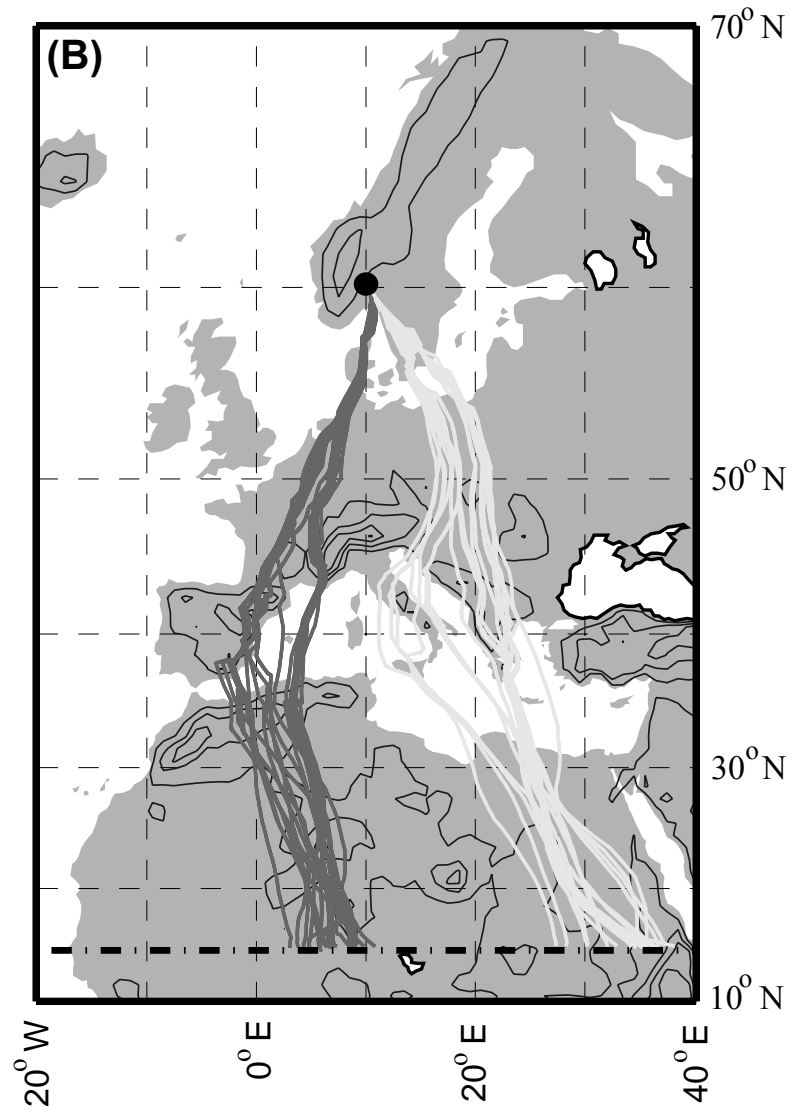
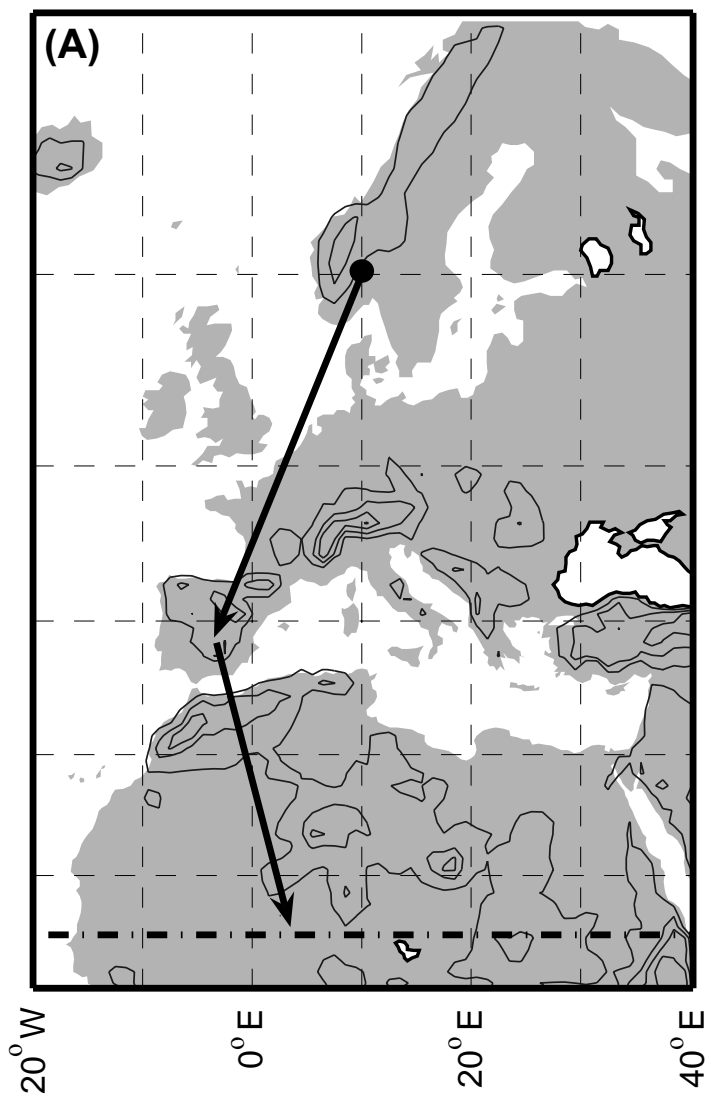


Figure 4.



→ Flight direction

Figure 5.