

Silke Bauer, Bruno J. Ens, and Marcel Klaassen. 2010. Many routes lead to Rome: potential causes for the multi-route migration system of Red Knots, *Calidris canutus islandica*. *Ecology* 91:1822–1831.

Appendix A. Optimal-migration model description.

We used dynamic programming (Houston and McNamara 1999, Clark and Mangel 2000) to find the sequence of migratory decisions maximizing the fitness of shorebirds under the environmental conditions encountered during spring migration. The model generally follows earlier versions (Weber et al. 1998, Bauer et al. 2008) but has been substantially modified for its application on Icelandic Knots. We therefore provide a full model description here.

We distinguished distinct sites including the wintering grounds, staging sites and the breeding grounds (see Fig. 1 for site locations and distances between sites). The migration period was divided into whole days t covering the period from 1st February to 31st July, i.e., 180 days.

We assumed that at time t , the expected future fitness F of a female shorebird, is a function of its fuel stores x , and its location i : $F(x, t, i)$. Body stores x may vary between 0, where the bird used in our simulations reaches a body mass of 110 g and dies of starvation, and x_{\max} , where it reaches the maximum fuel load of 3277 kJ at a body mass of 210 g. Thus, the energetic equivalent of 1 g body stores (and, thus, 1 x in the model) is 32.77 kJ and all other energy units, i.e., intake rates or energy expenditure, were expressed as g or g/d implicitly comprising this relation of energy content in body stores.

At the breeding or destination site N , the expected future fitness is $F(x, t, N)$. For each time step when the bird has not yet arrived at its destination, it has two behavioural options: either foraging at intensity u ($0 \leq u \leq 1$) or, if fuel stores permit, flying to another site.

Terminal Reward

Expected fitness is a function of arrival date, state upon arrival and expected fitness from future breeding attempts. Thus, birds at the destination (breeding grounds) can be expected to produce young in the current breeding season, $R(t)$, to have particular survival prospects, $S(x, t)$, and they may also expect fitness gains from future breeding attempts, R_0 .

$$F(x, t, N) = S(x, t) \cdot R(t) + R_0 \quad (\text{A.1})$$

The individual functions contributing to the fitness prospects of a bird have been determined from extensive empirical studies and will therefore be explained only shortly here (Tulp et al. 2009). Survival depends on time of arrival and body stores at arrival because the breeding grounds might still be snow-covered upon arrival and thus, offer only little or no food:

$$S(x, t) = \frac{\exp[-s_0 + s_1 t + s_2 x]}{1 + \exp[-s_0 + s_1 t + s_2 x]} \quad (\text{A.2})$$

Therefore, arriving late ensures a better survival. Also arriving with substantial body stores allows dealing with food-shortage. Based on empirical data we used the following estimates $s_0 = 28.61$, $s_1 = 0.246$ and $s_2 = 0.065$ (Ens et al. 2006).

The second component of the fitness function is this year's expected reproductive success, which mainly depends on arrival time:

$$R(t) = \alpha_0 \cdot \exp\left[\frac{-(t - \alpha_1)^2}{\alpha_2^2}\right] \quad (\text{A.3})$$

with $\alpha_0 = 2$, $\alpha_1 = 115.96$ and $\alpha_2 = 26.93$ (Ens et al. 2006). Thus, $R(t)$ indicates that there is only a rather narrow time window for successful start of breeding and this is mainly determined by the short period during which insects are sufficiently abundant for the chicks.

Birds that survive but fail to reach the breeding grounds in time have an expected fitness of R_0 – they may not reproduce this year but in the future. To resemble the approximated average life-time reproductive success of females in a stable population R_0 was set to 3.

Foraging

The maximum intake rate that a foraging shorebird may attain is site and time dependent ($g(u, i, t)$, g/d). The actual intake rate is determined by the foraging intensity u . How much of this intake rate ultimately is stored as body stores depends on the energy expenditure $e(i, t)$, (g_{fuel}/d), which mainly depends on ambient temperature (see below for site-specific estimates of intake rate and energy expenditure).

Maintaining fuel stores and foraging at certain intensity incurs a fitness cost in terms of increased risk of predation and injury (Witter and Cuthill 1993), which may vary between different locations. Thus, the total predation risk depends on a site-specific baseline predation risk, $\beta_0(i)$, the foraging intensity (u) dependent risk, $b_1(i) \cdot u^{m_1}$, and the mass (i.e., fuel-store x) dependent predation risk, $b_2(i) \cdot (x/x_{\text{max}})^{m_2}$, combined in summative manner since foraging or carrying high fuel loads can independently increase predation risk

$$m(x, u, i) = b_0(i) + b_1(i) \cdot u^{m_1} + b_2(i) \cdot (x / x_{\max})^{m_2} \quad (\text{A} \quad .4)$$

with m_1 and $m_2 = 4.0$, the site-specific coefficients for background predation risk $b_0 = 1.0^{-4}$, for foraging-intensity dependent predation risk $b_1 = 1.0^{-3}$, and for mass-dependent predation risk $b_2 = 1.0^{-2}$ such that adult survival over the period considered in the model was >90% (and thus approached the annual survival calculated by Boyd and Piersma 2001).

Thus, if the bird decides to forage, it should forage with an intensity u that yields the maximum expected fitness:

$$H_f(x, t, i) = \max_u [(1 - m(x, u, i)) \cdot F(x + ug(i, t) - e(t, i), t + 1, i)] \quad (\text{A.5})$$

Flying

Alternative to staying and foraging an individual could depart to the next site depending on its fuel stores x and the distance D (km) to the next site. Its fuel stores upon arrival at the destination x_a were calculated using

$$x_a = \left(\frac{c^2}{(c - (c(1 - (1 + x / x_{\max})^{-0.5} - D))^2) - 1} \right) \cdot x_{\max} \quad (\text{A} \quad .6)$$

where c is a flight range parameter which was calculated using

$$c = \frac{D_{\max}}{1 - (1 + x_f / x_{\max})^{-0.5}} \quad (\text{A.7})$$

and D_{\max} was the maximum flight range when dedicating fraction x_f of the maximum fuel load x_{\max} to flight. For the shorebirds in this study we used $x_f = x_{\max}$. We calculated D_{\max} by dividing the maximum fuel load by the flight costs f in terms of energy Kvist et al. 2001:

$$D_{\max} = \frac{x_{\max}}{f} \quad (\text{A.8})$$

If an individual decided to depart, it should fly to the site j yielding the maximum expected fitness at the destination:

$$H_d(x, t, i) = \max_j [F(x_a, t + (\sum_{z=i}^{j-1} D_z / v), j)] \quad (\text{A.9})$$

where v is flight speed, which was estimated at 1440 km/d (Piersma and van de Sant 1992).

The optimal decision is the behavioral alternative, foraging or departing, yielding the highest future expected reproductive success:

$$F(x, t, i) = \max[H_f(x, t, i), H_d(x, t, i)] \quad (\text{A.10})$$

The optimal decision matrix for all combinations of time, site, and body stores was used in subsequent forward simulations and thus, allowed us to track individual birds during their spring migration. Consequently, we predicted staging times and body store dynamics from these simulations and compared these with empirical data.

Using this optimal decision matrix, we followed individual birds on their migration to the breeding grounds using a Monte-Carlo simulation method. To this end, we let a population of 100 individuals with initial body stores start in a wintering site at $t = 0$. Thereafter, all individuals performed the optimal action according to their present body stores, site and time, i.e., migrating to site j or foraging with intensity u . The fuel gain at a given site was determined by a random

number and the probability distribution of $g(t, i)$. From these individual migrations, staging times on stop-over sites and expected fitness upon arrival were calculated.

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