

Mortality within the annual cycle: seasonal survival patterns in Afro-Siberian Red Knots *Calidris canutus canutus*

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Abstract Estimates of seasonal mortality for long-distance migrant birds are extremely challenging to collect and consequently reports are scarce. Determining when and where mortality occurs within the annual cycle is important for an understanding of population dynamics and the evolutionary drivers of long-distance migration. We collected data on seasonal survival in a mark–recapture study of colour-marked Red Knots *Calidris canutus canutus* in their main wintering area at tropical Banc d’Arguin, Mauritania, West Africa. Our study population breeds 9,000 km to the northeast on Taymyr Peninsula, central northern Siberia. Our results show that annual apparent survival decreased from 0.87 ± 0.01 (SE) in 2002–2005 to 0.78 ± 0.02 in 2006–2009. During the 3-year time-window between 2006 and 2009, additional resightings just before migration and after return to the wintering grounds allowed us to partition the year into two periods: the non-

breeding period on the Banc d’Arguin, and the migration and breeding period away from it. We estimated that, on the Banc d’Arguin, the 2-month apparent survival rate was 0.94 ± 0.01 , whereas 2-month survival approached unity during the rest of year. Hence, most mortality occurred on the tropical wintering grounds. We review the possible physiological and ecological stressors involved and discuss the generality of these results.

Keywords Annual survival · Banc d’Arguin · Long-distance migration · Mark–recapture models · Mauritania · Shorebird · Wader

Zusammenfassung

Die Verteilung der Sterblichkeit im Jahresverlauf: saisonale Überlebenswahrscheinlichkeiten bei Afro-Sibirischen Knutts *Calidris canutus canutus*

Das Sammeln von Daten zu saisonaler Sterblichkeit von Langstreckenziehern stellt Forscher vor große Herausforderungen. Dementsprechend werden solche Daten selten veröffentlicht. Um Populationsdynamiken und die evolutionären Einflussfaktoren auf die Entwicklung des Langstreckenzugs verstehen zu können, ist es jedoch wichtig, zu wissen, wann im Jahresverlauf die Sterblichkeit am höchsten ist. Wir haben Daten zu saisonaler Sterblichkeit im Rahmen eines Farbberingungsprojekts an Afro-Sibirischen Knutts *Calidris canutus canutus* in ihrem Hauptüberwinterungsgebiet an der Banc d’Arguin, Mauretanien, Westafrika, gesammelt. Diese Population brütet auf der 9,000 km entfernten Halbinsel Taymyr, im nördlichen Zentralsibirien. Unsere Ergebnisse zeigen, daß die lokale jährliche Überlebenswahrscheinlichkeit von $0.87 (\pm 0.01$ SE) in 2002–2005 auf $0.78 (\pm 0.02)$ in 2006–2009 gesunken ist.

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Im Zeitraum zwischen 2006 und 2009 hatten wir die Gelegenheit, sowohl kurz vor dem Abflug in die Brutgebiete als auch nach der Rückkehr in die Wintergebiete, zusätzliche Farbring-Beobachtungen durchzuführen. Diese haben es ermöglicht, das Jahr in zwei Zeiträume aufzuteilen—die Wintersaison an der Banc d'Arguin und die kombinierte Zug- und Brutsaison außerhalb der Banc d'Arguin -, und somit saisonale Überlebensraten zu berechnen. Wie berechneten, daß die Überlebenswahrscheinlichkeit an der Banc d'Arguin 0.94 (± 0.01 , über einen zweimonatigen Zeitraum) betrug, während die entsprechende Überlebenswahrscheinlichkeit im Rest des Jahres beinahe 1 war. Es scheint daher, daß die höchste Sterblichkeit im Jahresverlauf in den tropischen Überwinterungsgebieten stattfand. Wir erörtern diese Erkenntnisse vor dem Hintergrund möglicher physiologischer und ökologischer Stressfaktoren und diskutieren die allgemeine Gültigkeit unserer Ergebnisse.

Introduction

In the course of the annual cycle, migrants pass through a complex series of life-history stages including breeding, migratory movements, moult and the remainder of the non-breeding (or wintering) period (Murton and Westwood 1977; Newton 1998; Barta et al. 2008; McNamara and Houston 2008; Buehler and Piersma 2008). Events during these stages entail potential energetic and survival costs, and to maximise fitness, migrants should optimise the timing of the various stages (Ens et al. 1994; Sandberg and Moore 1996; Alerstam and Hedenström 1998; Drent et al. 2003; Greenberg and Marra 2004; Wingfield 2008). Identifying the seasons (and thus regions) when mortality is relatively high (or low) is important in helping to understand processes of population dynamics and the evolution of migration. Identifying the timing of demographic losses also provides important knowledge for the conservation of migratory species.

Studying seasonal survival is challenging because marked individuals must be monitored at different times of the year, and, in long-distance migrants, also at places far apart. Nevertheless, a number of studies have succeeded in breaking down annual (apparent) survival into seasonal components. Interestingly, so far, the findings have not been consistent among different species. For example, Sillett and Holmes (2002) have estimated elevated survival costs of active migration in a Nearctic–Neotropical passerine migrant. They studied the demography of breeding and non-breeding populations of the Black-throated Blue Warbler *Setophaga caerulescens*, and inferred survival during migration from annual survival estimates made on the basis of observations during the temperate breeding season and survival estimates across the tropical non-breeding season.

They suggest that 85 % of the annual mortality occurred during migration. Other studies, mainly on larger species like swans and geese, have not been able to detect higher mortality (exclusively) connected to migration, but some of these studies were not able to fully separate, e.g. breeding from migratory seasons, or did not find any seasonal variation at all (e.g. Clausen et al. 2001; Gauthier et al. 2001; Madsen et al. 2002; Hupp et al. 2008; Varner and Eichholz 2012).

We collected observations on a single population of individually marked Red Knots *Calidris canutus*, a long-distance migratory shorebird, during different periods throughout the annual cycle. The Afro-Siberian subspecies *C. c. canutus* (see Piersma 2007 for a review) spends a 2-month breeding season in north-central Siberia (Tomkovich and Soloviev 1996) and an 8-month non-breeding period in West African coastal wetlands (Piersma et al. 1992). Non-breeding populations of *canutus* Knots are concentrated mainly at the two largest West African intertidal areas, Banc d'Arguin, Mauritania (75 % of the population) and the Bijagós Archipelago, Guinea-Bissau (Piersma et al. 1992; Davidson and Piersma 2009). Excluding pre-departure fuelling periods, but including refuelling en route, northward and southward migration each take about 1 month. The 9,000 km distance between the non-breeding and breeding grounds is completed in two long-distance non-stop flights with stopovers in the German and Dutch Wadden Sea (Fig. 1). If prevailing winds during northward migration are unfavourable, up to 20 % of the wintering population use additional stopover sites along the Atlantic coast of France (Piersma et al. 1992; Leyrer et al. 2009; Shamoun-Baranes et al. 2010).

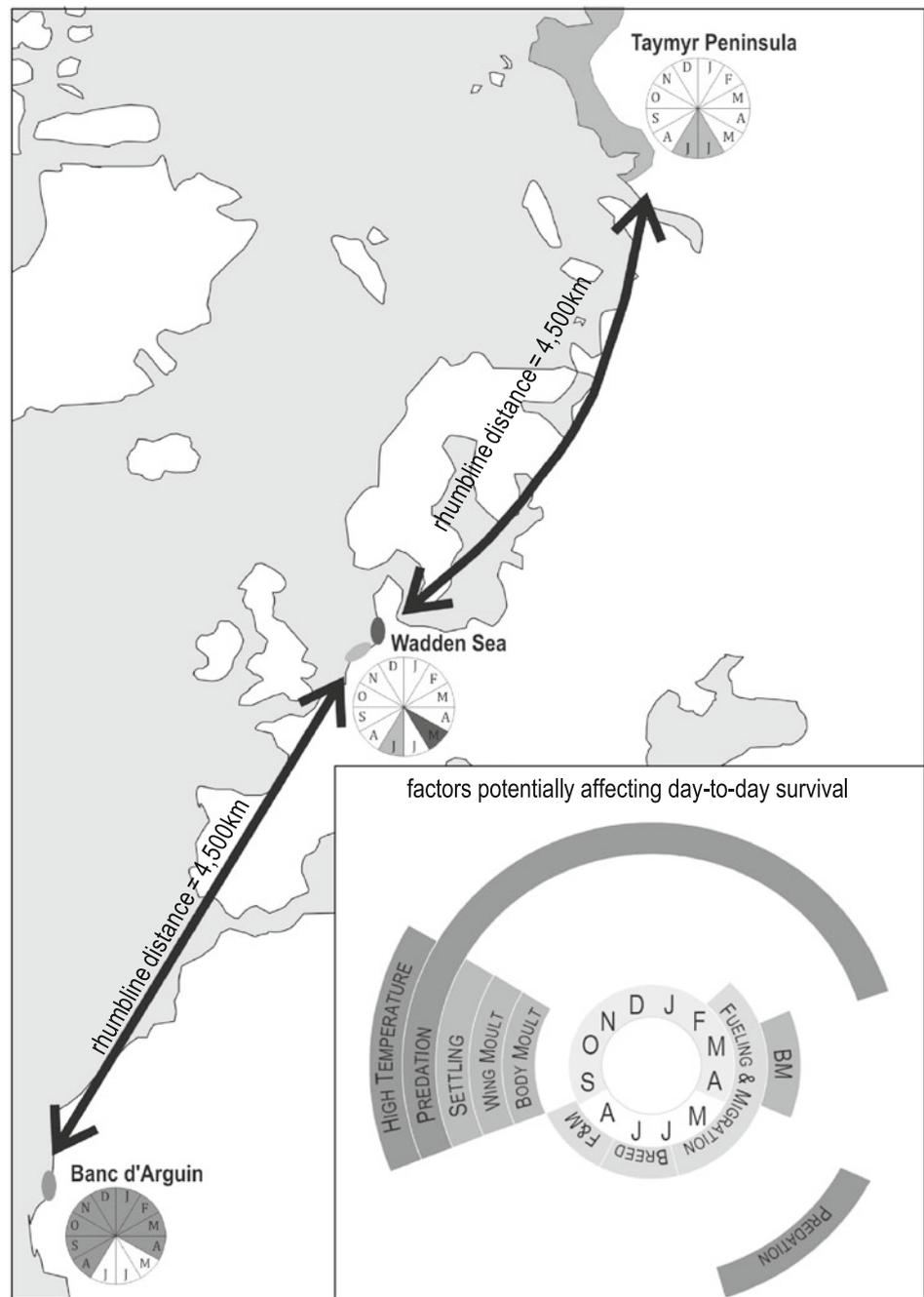
We monitored a single population of *canutus* Knots at their major non-breeding area, the Banc d'Arguin in Mauritania over an 8-year period between 2002 and 2009, and estimated annual apparent survival by colour-ringing individuals and collecting resightings each midwinter period. During a 3-year period between 2006 and 2009, we expanded our efforts in Mauritania to include resightings during April and August/September. Additional sampling periods allowed us to decompose annual survival rates into two periods: the 8-month non-breeding period in Africa, and the 4-month migration/breeding period in the northern hemisphere. We used mark-recapture methods to examine the hypothesis that survival differs between the migration and breeding period away from Banc d'Arguin and the stationary non-breeding period.

Methods

Study area and marking methods

Red Knots were captured and observed at Banc d'Arguin, Mauritania, West Africa. Our main study site was the

Fig. 1 Migratory cycle of Afro-Siberian Red Knots (*C.c. canutus*) with routes in Western Europe, central northern Asia and West Africa. The *canutus* subspecies spends an 8-month wintering period in West Africa, a 2-month breeding period in Siberia, with 1-month periods of north and southward migration, with the majority of birds stopping only in the Wadden Sea. *Inset* intrinsic [costs of reproduction (breed), fuelling and migration, body (BM) and wing moult, and establishing a winter home range (settling)] and extrinsic factors [predation, high temperatures] that may affect seasonal survival. The stationary part of the non-breeding period [wintering (Sep - Apr)] is shaded in light grey



high-tide roost of Abelgh Eiznaya on the western shores of Iwik Peninsula (19°54'N 16°17'W; see Fig. 2 in Leyrer et al. 2006). Using mist-nets, we captured Red Knots at spring high tides and dark nights during new moon lunar phases between mid-November and late December of 2002–2008. At first capture, each Red Knot was individually marked with a metal ring of the Dutch ringing scheme ('Vogeltrekstation Arnhem') and a unique combination of four colour-rings and a plain leg flag (Piersma and Spaans 2004). Birds were aged by plumage characteristics in two

age-classes according to Prater et al. (1977), distinguishing hatch-year birds (juveniles <12 months) and older birds (>12 months). A drop of blood was collected from the brachial vein and stored in 96 % ethanol for subsequent molecular sexing. We only included sexed individuals in our analysis. Red Knots captured during 2002–2006 were sexed with primers P2/P8 (Griffiths et al. 1998; verified for Red Knots by Baker et al. 1999). To avoid potential sexing errors due to length polymorphisms in the Z-introns of the CHD-gene (Casey et al. 2009; Schroeder et al. 2010), Red

Knots captured from 2007 to 2009 were sexed with primers 2602F/2669R (Fridolfsson and Ellegren 1999; modified for shorebirds by O. Haddrath). A comparison between the two methods showed that the previous method resulted in an error rate of about 5 %, with a bias towards males being incorrectly sexed as females. Sex was not a determining factor in this analysis (see below) and our error was relatively small, so we decided not to make adjustments for any incorrectly sexed individuals.

Sample sizes and observations of Red Knots

Annual and seasonal apparent survival were estimated using capture–resighting data from colour-ringed Red Knots caught at the Abelgh Eiznaya high-tide roost, but observed throughout the entire ca. 35-km² study area at Iwik Peninsula. A total of 1,007 birds were individually marked during the seven winters of 2002–2008. To estimate annual apparent survival, we recaptured and resighted Knots during the winters of 2003–2009 during annual 3-week expeditions in November/December. To estimate seasonal apparent survival, we considered observations of marked birds from additional expeditions at the start and end of each non-breeding season during a 3-year period: early August–late September 2006, mid- to late April 2007, mid-August–early September 2007, late March–mid-April 2008, late August–mid-September 2008, mid- to late April 2009. Red Knots marked before winter 2006 and not seen during the second study period were not included in this analysis, and estimates of seasonal survival were thus based on a reduced subset of 804 birds.

Observation effort was greatest during the winter expeditions and lower but comparable between late summer and spring (Table 1). Late summer/early autumn expeditions were timed to coincide with the Red Knots' return period from the breeding grounds (Piersma et al. 1992), but an unknown percentage of Red Knots might not yet have returned when we concluded our observations in late September. Counts in our study area in late summer 2006 showed that Red Knot numbers increased from ca. 7,500 in mid-August to ca. 14,000 in late August. Maximum counts of non-breeding birds in our study area during midwinter averaged ~18,000 Red Knots (Piersma and Leyrer, unpublished data). To reduce the probability that individuals were unavailable for being resighted because they had already migrated, observations in spring were made well before departure of Red Knots from our study area for northward migration (Piersma et al. 1990).

Data analysis

Apparent survival (ϕ) and the probability of encounter (p) were estimated from live encounter data based on

captures and resightings using Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992) for annual intervals with equal time steps and seasonal periods with unequal time steps. To improve precision of the estimates, some a priori decisions were made to reduce the number of parameters that had to be estimated. Models were constructed and run in program MARK (v.6.0; White and Burnham 1999), and in R (v.2.14.0; R Core Team 2013) using the RMark package (v.2.1.14; Laake et al. 2012). Model selection was based on QAIC_c.

An initial analysis of annual survival using the full 8-year dataset showed that models including time-dependent variation among years in apparent survival ϕ had high AIC scores and low Akaike weights, and that sparse data led to problems with estimation of ϕ and p . We were less interested in annual variation in ϕ for this study, and opted to exclude time as a factor for ϕ , but not for p . Recent studies on food availability at the study site has indicated that prey quality might have decreased in recent years (van Gils et al. 2013). We thus tested whether survival differed between the two periods before and during measuring seasonal survival (2002–2005 and 2006–2009, respectively) and added “period” as a factor influencing annual survival. Field efforts were greater in later years and resighting skills improved in the course of this study due to observer training and better local field knowledge, therefore, probability of encounter p was modelled with variation among years, but not between age- or sex-classes.

On the Banc d'Arguin, Red Knots occur in open tidal habitats where they are always very visible. All birds foraged on mudflats during low tide and assembled at communal roosts at high tide. We modelled apparent survival as a function of three factors: age at capture (juveniles vs. adults), sex (male vs. female), and an effect of time-since-marking (tsm) (Sandercock 2006). Time-since-marking was included to test whether newly marked individuals differed in apparent survival during their first year (ϕ^1) compared with subsequent years (ϕ^{2+}).

Apparent survival might be lower after first capture if we had either an unknown proportion of transient birds in our study population or a number of individuals experienced a higher mortality immediately after catching due to capture and handling stress. We also occasionally found carcasses of newly marked birds that had been killed by feral cats after release, potentially as a consequence of being captured and handled. Because our main interest was not to estimate mortality associated with capturing and handling, these birds were censored from the analyses. The tsm effect was included for each age-class (juveniles and adults). Juvenile Red Knots become adults at the end of their second calendar year, and low juvenile survival could be due to age, tsm, or both. Goodness-of-fit was tested for

Table 1 Number of observation sessions in the study area at Iwik peninsula, Banc d’Arguin, Mauritania in different seasons between 2003 and 2009

	2003	2004	2005	2006	2007	2008	2009
Winter	47	75	83	229	96	118	117
Spring					37	11	16
Autumn				92	22	17	

Each observation session covers a single period of time (1–3 h) spent by one observer in a sub-area within the study area (for sub-areas, see Leyrer et al. 2006)

our global starting model $\phi_{\text{age} \times \text{tsm} \times \text{sex} \times \text{period}} p_{\text{year}}$ with the median- \hat{c} test implemented in MARK, and \hat{c} was adjusted with the estimated $\hat{c} = 1.02 \pm 0.00$ SE. We present model averaged estimates of annual apparent survival.

Our data to model seasonal variation in apparent survival ϕ and encounter rates p spanned only 3 years and we therefore excluded year as a factor from both parameters. Due to differences in observation effort, resighting probability p was modelled with season-dependence among expeditions in late spring (April), late summer/early autumn (August/September), and winter (December) (Table 1). We set unequal time steps to estimate 2-month rates of apparent survival and tested two different scenarios: (1) dividing the year into three seasons: a 5-month winter (December–April), a 4-month migration + breeding (May–August), and a 3-month autumn (September–November), and (2) dividing the year into two seasons: an 8-month stationary non-breeding season (September–April) versus a 4-month migration + breeding season (May–August).

Migratory behaviour differed between juveniles and adults, as the former generally did not leave on northward migration and remained at non-breeding areas during the boreal summer (van Dijk et al. 1990, personal observation). We thus included age-class as a factor for ϕ in our seasonal models and juveniles were treated differently in estimating ϕ until the winter preceding their first northward migration (in their 3rd calendar year). A tsm effect on seasonal survival was tested for newly ringed individuals during the season following the marking event (December–April). Individuals marked before December 2006 were included by treating the first encounter within the study period (summer 2006 until spring 2009) as a ‘marking event’, but because they had already returned to the area, we excluded a tsm-effect for those individuals. Juvenile birds were considered adults from the following winter on, and the effect of age on survival could only be tested in models including a tsm-effect. We pooled sexes in the seasonal models because our results from annual models showed little evidence of sex differences. Goodness of fit was tested using the median- \hat{c} test in MARK for the starting

model $\phi_c^1 \phi_{\text{age}+3\text{seasons}}^{2+} p_{3\text{seasons}}$, and \hat{c} was adjusted with the estimated $\hat{c} = 1.31 \pm 0.00$ SE.

Some of our estimates of seasonal survival approached unity. We performed four types of sensitivity analyses to determine whether survival was close to the boundary of 1, or if our data were too sparse to estimate this parameter. We first fitted reduced models to compare estimated survival values. Second, we assessed convergence of the models using the alternate optimisation method based on simulated annealing in MARK, which is more likely to find the global instead of a local maximum (Cooch and White 2011). Third, we fitted the best model using a Bayesian procedure, the Markov chain Monte Carlo (MCMC) estimation implemented in MARK, and compared the mean, median and mode of the MCMC estimates with the parameters of the same model fitted with maximum-likelihood procedures. Last, we ran our models through the data-cloning routine implemented in MARK (Cooch and White 2011). Encounter histories were cloned 100 times and two criteria were used to determine if the parameter of a model were estimable: if a parameter is estimable, the ratio of the SE for a given parameter estimated from the cloned and original data should be ~ 10 , and the 95 % CI should be smaller in the cloned versus the original data. We used profile likelihood CI for all parameters because this procedure performs better for parameters close to the boundaries of zero and one.

Results

Annual survival

The minimum QAIC_c model describing annual apparent survival included an effect of tsm and indicated difference in survival ϕ between the periods of 2002–2005 and 2006–2009 (Table 2). Model averaged annual estimates of adult survival in the interval after first marking (ϕ^1) in 2002–2005 were 0.82 ± 0.02 SE (95 % CI = 0.77–0.86) and 0.71 ± 0.04 (0.63–0.78) in 2006–2009. In subsequent years (ϕ^{2+}), adult survival was 0.87 ± 0.01 (0.84–0.90) for 2002–2005 and 0.78 ± 0.02 (0.74–0.82) for 2006–2009

Table 2 Model selection results for estimation of annual apparent survival (Φ) and resighting probability (p) for Red Knots *C. c. canutus* at Banc d'Arguin, Mauritania, 2002–2009

Model	NP	QDeviance	QAIC _c	Δ QAIC _c	QAIC _c weight
$\phi_{\text{period}}^1 \phi_{\text{period}}^{2+} P_{\text{year}}$	10	688.71	4,737.26	0	0.53
$\phi_{\text{age+period}}^1 \phi_{\text{period}}^{2+} P_{\text{year}}$	11	688.25	4,738.82	1.56	0.24
$\phi_{\text{age+sex+period}}^1 \phi_{\text{sex+period}}^{2+} P_{\text{year}}$ ^a	12	688.09	4,740.68	3.42	0.10
$\phi_{\text{age+period}} P_{\text{year}}$	10	692.98	4,741.53	4.26	0.06
$\phi_{\text{period}} P_{\text{year}}$	9	696.48	4,743.01	5.75	0.03
$\phi_{\text{age+sex+period}} P_{\text{year}}$	11	692.78	4,743.35	6.08	0.03
$\phi_{\text{sex+period}} P_{\text{year}}$	10	696.36	4,744.91	7.65	0.01
$\phi_{\text{const}}^1 \phi_{\text{const}}^{2+} P_{\text{year}}$	9	703.63	4,750.16	12.90	0
$\phi_{\text{age}}^1 \phi_{\text{const}}^{2+} P_{\text{year}}$	10	703.09	4,751.64	14.37	0
$\phi_{\text{age}} P_{\text{year}}$	9	705.91	4,752.45	15.18	0
$\phi_{\text{const}} P_{\text{year}}$	8	708.36	4,752.87	15.61	0
$\phi_{\text{age+sex}} P_{\text{year}}$	10	705.59	4,754.14	16.87	0
$\phi_{\text{sex}} P_{\text{year}}$	9	708.13	4,754.66	17.40	0

Model parameters: ϕ^1 = survival in first year after marking, ϕ^{2+} = survival in subsequent years, const = constant, age = adult/juvenile, sex = female/male, period = time span 2002–2005 vs. 2006–2009. Model statistics include: number of parameters (NP), QDeviance, Akaike's information criterion corrected for small sample size and overdispersion (QAIC_c), Δ QAIC_c, and QAIC_c weight

^a The goodness of fit was tested for the starting model $\phi_{\text{age+sex+period}}^1 \phi_{\text{sex+period}}^{2+} P_{\text{year}}$, and \hat{c} was adjusted to 1.02

(Table 3). Juveniles tended to have a slightly lower annual apparent survival of 0.81 ± 0.03 (0.75–0.86) for 2002–2005, and 0.69 ± 0.04 (0.61–0.77) for 2006–2009. We found no support for sex-specific survival (Table 2).

Seasonal survival

The 12 models tested based on our assumptions and selection criteria are shown in Table 4; highlighted models contain no non-estimable parameters. Time-since-marking was the main parameter explaining seasonal survival. The best model suggested that survival was distributed unequally throughout the year, and was lower during the stationary 8-month period at Banc d'Arguin $\phi_{\text{Sepndash;Apr}}$ 0.94 ± 0.01 (0.92–0.95; 2-month survival) than during the 4-month migration + breeding period $\phi_{\text{Mayndash;Aug}}$ $0.99 \pm 0.43 \times 10^{-4}$ (0.97–0.99; 2-month survival) (Table 5). Models in which the year was divided into three seasons either contained non-estimable parameters or scored high AIC values. Survival was lowest in the first season after catching and marking ($\phi_{\text{Dec-Apr}}^1$ 0.86 ± 0.02 ; 0.81–0.89; 2-month survival) as in the analysis of annual survival estimates.

A seasonal survival rate near unity for the combined migration and breeding period was unexpected. The fitting of reduced models with constant resighting probabilities to test the sensitivity of the estimates of $\phi_{\text{Mayndash;Aug}}$ showed that estimates remained unchanged. Using the alternate

optimisation method based on simulated annealing did not change our model selection or estimates either. We then compared the mean, median and mode of the MCMC estimation, and found that the 2-month $\phi_{\text{Mayndash;Aug}}$ remained high (mean \pm SD, 0.98 ± 0.12 ; median 0.99; mode 0.99, for the best model in Table 4); all other estimates for ϕ^1 and ϕ^{2+} only differed in the third decimal place. Last, we used the data cloning routine implemented in MARK. For the best model, the estimates of survival remained similar, standard errors and confidence intervals of our cloned estimates were smaller than of our original estimates (Table 5). Reductions in confidence intervals indicated that MARK had correctly estimated the parameter, although probably biased towards the boundary value of 1. We present all tested models in Table 4, and highlighted the ones where all parameters were estimable.

Discussion

For a shorebird the size of the Red Knot, the survival estimates found are relatively high (Sandercock 2003), and establish that Red Knots both show strong site fidelity to non-breeding sites and generally have high survival rates (Brochard et al. 2002; Baker et al. 2004; Leyrer et al. 2006, 2012; Spaans et al. 2011). The 9 % decline in annual apparent survival detected between the time spans of 2002–2005 and 2006–2009 requires further in-depth

Table 3 Model averaged annual estimates of apparent survival (ϕ) and resighting probabilities (p) with standard errors and 95 % confidence intervals of *canutus* Red Knots at a non-breeding site in Banc d’Arguin, Mauritania, West Africa, in 2003–2009

Period	Estimate \pm SE	95 % CI
2002–2005		
ϕ^1	0.82 \pm 0.02	0.77–0.86
ϕ^{2+}	0.87 \pm 0.01	0.84–0.90
ϕ^j	0.81 \pm 0.03	0.75–0.86
2006–2009		
$\phi^1 \phi^{2+}$	0.71 \pm 0.04	0.63–0.78
	0.78 \pm 0.02	0.74–0.82
ϕ^j	0.69 \pm 0.04	0.61–0.77
Resighting probabilities p		
2003	0.24 \pm 0.04	0.18–0.32
2004	0.37 \pm 0.03	0.32–0.43
2005	0.48 \pm 0.03	0.43–0.53
2006	0.52 \pm 0.03	0.47–0.58
2007	0.66 \pm 0.03	0.61–0.71
2008	0.69 \pm 0.03	0.63–0.75
2009	0.63 \pm 0.04	0.55–0.70

ϕ^1 = adult annual apparent survival in first year after marking, ϕ^{2+} = adult annual apparent survival in subsequent years, ϕ^j = juvenile annual apparent survival

studies. We have indications that in recent years a decrease in local food quality has impacted on the survival of Red Knots (van Gils et al. 2013).

A combination of factors could have contributed to the differences in survival between the first year after marking and later years (Sandercock and Jaramillo 2002). Capture and handling of Red Knots (and other shorebird species) in tropical environments may make birds susceptible to developing capture myopathy (Rogers et al. 2004), which can be immediately fatal or make individuals prone to predation after release. Time-since-marking effects could also have been due to the capture of transient birds passing through our study area during midwinter. The non-breeding distribution of *canutus* Knots extends further south to other areas in equatorial Africa including the Bijagós Archipelago, Guinea-Bissau (Piersma et al. 1992), and a subset of marked birds may have permanently emigrated from our study population.

In contrast to results from the previous study on Black-throated Blue Warblers (Sillett and Holmes 2002), we found that the period of lowest apparent survival within the annual cycle in our tropical wintering species occurred during the wintering period. Admittedly, the 3-year period (which evidently comprises two summers) when we could decompose annual survival into seasonal components is a

Table 4 Model selection for seasonal estimates of apparent survival (ϕ) and recapture probability (p) for *canutus* Red Knots wintering at Banc d’Arguin, Mauritania, 2006–2009

Model	NP	QDeviance	QAICc	Δ QAICc	QAICc weight
$\phi_c^1 \phi_{2seasons}^{2+} p_{3seasons}$	6	417.25	2,739.56	0	0.27
$\phi_{age}^1 \phi_{2seasons}^{2+} p_{3seasons}$	7	416.26	2,740.58	1.03	0.16
$\phi_c^1 \phi_{3seasons}^{2+} p_{3seasons}$	7	416.37	2,740.69	1.14	0.15
$\phi_{age}^1 \phi_{3seasons}^{2+} p_{3seasons}$	8	415.38	2,741.72	2.17	0.09
$\phi_c^1 \phi_{age+2seasons}^{2+} p_{3seasons}$	7	417.55	2,741.88	2.32	0.08
$\phi_c^1 \phi_c^{2+} p_{3seasons}$	5	422.18	2,742.47	2.91	0.06
$\phi_{age}^1 \phi_{age+2seasons}^{2+} p_{3seasons}$	8	416.96	2,743.30	3.75	0.04
$\phi_c^1 \phi_{age+3seasons}^{2+} p_{3seasons}$	8	417.01	2,743.36	3.80	0.04
$\phi_{age}^1 \phi_c^{2+} p_{3seasons}$	6	421.21	2,743.52	3.96	0.04
$\phi_c^1 \phi_{age}^{2+} p_{3seasons}$	6	422.11	2,744.41	4.85	0.02
$\phi_{age}^1 \phi_{age+3seasons}^{2+} p_{3seasons}$	9	416.52	2,744.89	5.33	0.02
$\phi_{age}^1 \phi_{age}^{2+} p_{3seasons}$	7	421.07	2,745.40	5.84	0.01

ϕ^1 = apparent survival in first winter after marking (comprises December–April), ϕ^{2+} = apparent survival in subsequent seasons/years, 2 seasons = year divided in two seasons (stationary non-breeding and migration + breeding), 3 seasons = year divided into three seasons (winter, migration + breeding, autumn), age = juvenile/adult, c = constant. Juvenile Red Knots were treated as adults from the winter preceding the first migration + breeding season onwards. Given are number of estimable parameters (NP), QDeviance, Akaike’s information criterion values corrected for small sample size (QAIC_c), Δ QAIC_c and QAIC_c weight. Models in bold contain no non-estimable parameters (see “Materials and Methods”). The goodness-of-fit (GOF) was tested for model $\phi_c^1 \phi_{age+3seasons}^{2+} p_{3seasons}$ and \hat{c} was adjusted to 1.31

Table 5 Estimates of 2-month apparent survival (ϕ) and recapture probability (p), standard errors, and 95 % confidence intervals for *canutus* Red Knots wintering at Banc d'Arguin, Mauritania, West Africa, in 2006–2009

Parameter	Original estimates		Data-cloning estimates	
	$\phi \pm \text{SE}$	95 % CI	$\phi \pm \text{SE}$	95 % CI
Survival				
ϕ^{2+} at Banc d'Arguin	0.94 ± 0.01	0.92–0.95	0.941 ± 0.0007	0.939–0.942
ϕ away from Banc d'Arguin	$0.99 \pm 0.43 \times 10^{-4}$	0.97–0.99	$0.999 \pm 3.77 \times 10^{-6}$	0.9997–0.9999
ϕ^1 at Banc d'Arguin	0.86 ± 0.02	0.81–0.89	0.857 ± 0.002	0.853–0.860
Recapture probability				
p December	0.60 ± 0.03	0.55–0.65		
p April	0.21 ± 0.02	0.18–0.24		
p August	0.11 ± 0.01	0.08–0.13		

Survival estimates are based on the best-supported model from Table 4, and given for both the original data and the data-cloning procedure (see “Materials and methods”)

Time-since-marking effect: ϕ^1 = survival during the first winter after marking, ϕ^{2+} = survival during subsequent winters. As birds were caught in Decembers only, an effect after marking was only possible in winter

short period for estimating even annual survival. Thus, we consider the question: how robust are our results?

Apparent annual survival during the 3-year period (0.76) was comparable to the estimate based on the corresponding time span (2006–2009) of the 8-year data series (0.78). Furthermore, our sensitivity analyses indicated that our data were not sparse and that the demographic parameters were estimable with our approach. In the following paragraphs, we discuss climate, predation, food, and competition as potential explanations for the relatively low overwinter survival of Red Knots at Banc d'Arguin in 2006–2009.

During the 2006–2009 period, no major environmental disturbances were observed at the key staging sites of the Afro-Siberian Red Knot population along the Atlantic coast or in the Wadden Sea (Leyrer, unpublished observation). Earlier studies showed that Afro-Siberian Red Knots make use of emergency staging sites during northward migration when weather conditions are adverse (van de Kam et al. 2004; Leyrer et al. 2009; Shamoun-Baranes et al. 2010). Relatively long-lived, some Red Knots may terminate migration or skip breeding to enhance their survival chances if conditions are unfavourable. In a study on the impacts of wind on migration schedules from wintering areas of similarly long-distance migrating Bar-tailed Godwits *Limosa lapponica baueri*, Conklin and Battley (2011) observed high return rates even in individuals that departed off-schedule. This suggests that individuals are able to respond flexibly to unfavourable circumstances such as sustained head-winds during departure.

At Banc d'Arguin, Red Knots might be impacted by multiple stress factors during the non-breeding season (Fig. 1). Of these factors, predation by raptors, primarily

Lanner *Falco biarmicus* and Barbary Falcons *Falco peregrinoides*, is unlikely to play a *direct* role because predation at Banc d'Arguin accounts for a mere 0.8 % of adult annual mortality (van den Hout et al. 2008). However, Red Knots may compromise foraging opportunities or other behavioural decisions under the threat of predation risk (van den Hout, unpublished data). High winter mortality may also reflect a combination of pressures acting on the birds caused by competition and physiological stress (Fig. 1). Leyrer et al. (2012) showed that, within the study area at Banc d'Arguin, differences in winter habitat quality lead to differences in apparent survival. Habitat-specific survival was explained by relatively high intraspecific competition after return from the breeding grounds, expressed either in reduced survival during settlement or with a delay in the course of winter. Maintenance of a positive energy balance during the non-breeding period at Banc d'Arguin may also be compromised by food quality. One of the two staple prey species (*Loripes lucinalis*) causes diarrhoea when consumed in great quantity (van Gils et al. 2012; Oudman et al. 2013). Variations in annual apparent survival correlate with changes in the abundances of the two staple prey species, likely because, depending on their precise availability, intake rates might be constrained by the toxic load of *L. lucinalis* (van Gils et al. 2013).

When returning to Banc d'Arguin, Red Knots immediately start to moult, replacing both flight and body feathers (unpublished data) at a time when ambient temperatures are at seasonal maxima. Average maximum August/September temperature at Banc d'Arguin is 28–31 °C (Wolff and Smit 1990), but daily maximum temperatures are regularly in the high 40s °C with high humidity (Leyrer,

unpublished data). Moulting is a physiologically challenging process that generates heat (Lindström et al. 1993; Klaassen 1995; Portugal et al. 2007; Cyr et al. 2008; Vézina et al. 2009). Under prevailing climatic conditions, moulting Red Knots could be constrained by their capacity to dissipate heat, at a risk of hyperthermia. Even mild hyperthermia can have long-term negative effects on organismal performance (Speakman and Krol 2010). During moulting, Knots appear to down-regulate costly immune functions (Buehler et al. 2008). Red Knots thus face a series of potential internal and external stressors upon arrival after an 18,000-km return migration (Fig. 1) and an energetically challenging breeding season in the high Arctic (Piersma et al. 2003). Seasonal carry-over effects may well contribute to the observed higher winter mortality (Harrison et al. 2011).

Our findings show that survival can be lowest during the stationary non-breeding periods not only in birds wintering in temperate latitudes, where weather conditions can be harsh, but also in tropical environments with a benign climate. Given the short study period and the stochastic nature of mortality events in a long-lived shorebird species, we naturally would not conclude that all mortality occurs at Banc d'Arguin. Yet, this might have been the case in our 3-year study if Red Knots encountered benign conditions en route during migration and at the breeding grounds. Longer time series are needed to determine long-term patterns in seasonal survival, to identify key times and sites of stress and constraint (Buehler and Piersma 2008), and to inform studies on the possible flexibility of migratory behaviour (Piersma 2007, 2011). With the rapid loss of habitats or resources along the flyways (Baker et al. 2004; van Gils et al. 2006; Piersma 2007; Kraan et al. 2010; Rogers et al. 2010; Battley et al. 2012), conservationists greatly depend on knowledge of seasonal demography to improve conservation strategies for long-distance migrating populations.

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