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ORIGINAL ARTICLE

Negotiating the northern edge of a nonbreeding distribution: a case of winter mortality in Eurasian Spoonbills

Theunis Piersma[1,2,3] · **Sven Prins**[4] · **Anne Dekinga**[2]

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Abstract

During a cold spell from 6 to 14 February 2021, we monitored the fate of Eurasian Spoonbills *Platalea leucorodia leucorodia* on Schouwen-Duiveland, province of Zeeland, The Netherlands. On 6 February 2021, average daily air temperature dropped to below 0 °C, and for the next 8 days frost was maintained, with thaw arriving on 15 February. As the wind picked up as well, (human) wind chill temperatures dropped to below − 10 °C during this entire period. The victims at the Levensstrijd wetland near Zierikzee, fully ice covered within a day after the drop in temperatures, were all juvenile (i.e. born in 2020). They stood waiting before dying on 12–13 February (six were found and collected). They remained at Levensstrijd despite one marked individual among them having previously been at sites which kept having open water during the cold spell. This included the canals near Burgh-Haamstede (ca. 8 km away) where 26 birds (mostly adult) were foraging during the cold spell. Nevertheless, two spoonbills were found dead here too, one of which was an adult. The eight collected carcasses were stored frozen for subsequent analysis of body composition. The winter victims weighed 71% (4 males)–76% (4 females) of the asymptotic body mass predicted for growing juveniles. The dissected specimens showed no fat, their masses (and those of the organs and muscles as well) tightly correlating with body size. The mass fractions of the different body parts of the winter-starved spoonbills (compared to 'normal') were high for lungs (i.e. no loss), medium for leg muscles (a loss of 20%) and low for the flight muscles and the internal organs heart, stomach, intestines and liver (losses of 40–65%). We propose that the cold spell victims had shifted from using fat to using protein as their reserve fuel, at which point air temperatures of -5 °C and wind speeds of 8–10 m/s must have induced hypothermia and death. It did not kill birds in nearby flocks with access to open water, birds which must have had a better body condition and could still rely on fat as fuel. This study demonstrates the susceptibility of especially young spoonbills to food becoming locally unavailable during frost events during which surface waters freeze over. We are puzzled by the lack of movements to nearby places with open water and food when Levensstrijd froze solid, as the birds were capable of flight even on the day before being found dead. Does lethargy and the strong cold winds explain it, or do social inhibitions (by the victims) and despotic behaviours (by the surviving adults at the open water site) play a role? Although it is likely that juvenile, rather than adult, spoonbills will be the first to winter on a shifting northern edge of the nonbreeding distribution, these youngsters are also most at risk when cold spells hit.

Keywords Body composition · Climate change · Demography · Despotic behaviour · Frost · Mortality · Natural selection · *Platalea leucorodia* · Starvation

Zusammenfassung

Zurechtkommen am nördlichen Rand der Verbreitung außerhalb der Brutzeit: ein Fall von Wintersterblichkeit bei Löfflern

Während eines Kälteeinbruchs vom 6. bis 14. Februar 2021 haben wir das Schicksal der Löffler *Platalea leucorodia leucorodia* auf Schouwen-Duiveland, Provinz Zeeland, Niederlande, beobachtet. Am 6. Februar 2021 sank die durchschnittliche tägliche Lufttemperatur auf unter 0 °C, und in den folgenden acht Tagen herrschte weiterhin Frost, bis am 15. Februar Tauwetter einsetzte. Da auch der Wind auffrischte, sank die (menschlich) gefühlte Temperatur während des gesamten

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Zeitraums auf unter minus 10 °C. Die im Feuchtgebiet Levensstrijd nahe Zierikzee, das innerhalb eines Tages nach dem Temperatursturz vollständig vereist war, gefundenen Vögel waren allesamt Jungtiere (d. h. im Jahr 2020 geboren). Sie warteten, bis sie am 12. und 13. Februar starben (sechs wurden gefunden und eingesammelt). Sie blieben in Levensstrijd, obwohl ein markiertes Individuum unter ihnen zuvor an Orten gewesen war, die während des Kälteeinbruchs weiterhin offenes Wasser hatten. Dazu gehörten die Kanäle bei Burgh-Haamstede (ca. 8 km entfernt), wo 26 Vögel (meist adulte) während des Kälteeinbruchs auf Nahrungssuche waren. Dennoch wurden auch hier zwei Löffler tot aufgefunden, darunter ein erwachsener Vogel. Die acht gesammelten Kadaver wurden für die anschließende Analyse der Körperzusammensetzung tiefgefroren aufbewahrt. Die Vögel wogen 71% (4 Männchen) bis 76% (4 Weibchen) der für heranwachsende Jungvögel vorhergesagten asymptotischen Körpermasse. Die sezierten Exemplare wiesen kein Fett auf, ihre Körpermasse (und auch die der Organe und Muskeln) korrelierte eng mit der Körpergröße. Die Massenanteile der verschiedenen Körperteile der im Winter verhungerten Löffler (im Vergleich zu „normalen “) waren hoch für die Lunge (d.h. kein Verlust), moderat für die Beinmuskulatur (ein Verlust von 20%) und niedrig für die Flugmuskeln und die inneren Organe Herz, Magen, Darm und Leber (Verluste von 40-65%). Wir vermuten, dass die Opfer des Kälteeinbruchs von der Verwendung von Fett auf die Verwendung von Eiweiß als Reservetreibstoff umgestiegen sind. Zu diesem Zeitpunkt müssen Lufttemperaturen von −5 °C und Windgeschwindigkeiten von 8–10 m/s zu Unterkühlung und Tod geführt haben. Vögel mit Zugang zu offenem Wasser, die vermutlich eine bessere Körperkondition hatten und wohl noch auf Fett als Brennstoff zurückgreifen konnten, waren nicht betroffen. Diese Studie zeigt, wie empfindlich insbesondere junge Löffler darauf reagieren, wenn bei Frostereignissen, bei denen die Oberflächengewässer zufrieren, lokal keine Nahrung mehr verfügbar ist. Es ist rätselhaft, warum die Vögel nicht zu nahe gelegenen Orten mit offenem Wasser und Nahrung flogen, als Levensstrijd zugefroren war, denn die Vögel waren noch am Tag vor dem Auffinden des Todes flugfähig. War es aufgrund von Lethargie und den starken kalten Winden, oder spielen soziale Hemmungen (bei den Opfern) und despotische Verhaltensweisen (bei den überlebenden Altvögeln am offenen Wasser) eine Rolle? Obwohl wahrscheinlich ist, dass eher die Jungvögel als die erwachsenen Löffler die ersten sind, die an einem sich verschiebenden nördlichen Rand der Winterverbreitung überwintern, sind diese Jungvögel auch am meisten gefährdet, wenn es zu Kälteeinbrüchen kommt.

Introduction

Birds thrive in places where there is enough food, where they can maintain water and heat balances, and where they can avoid the detrimental effects of predators and parasites (Piersma 2012). The poleward edges of species distributions are likely to be determined by sufficient availability of food and the avoidance of hypothermia (Root 1988). To 'explain' range limits, the seeming simplicity of approximating energy expenditure from body mass on the basis of allometric equations (Scholander et al. 1950; Tracy 1972), combined with the idea that these expenditure levels are bound to maximum levels (e.g. Drent and Daan 1980; Peterson et al. 1990), has invited a suite of comparative studies (e.g. Buckley et al. 2018; Khaliq et al. 2014, 2017). These, in turn, have met with serious methodological criticism (Boyles et al. 2019). Reviewing a population dynamic, rather than a comparative energetic, perspective on range limitations, Gaston (2009) concludes that "empirical studies have lagged substantially behind developments in theory". Indeed, there are rather few studies specifying the interactions between environmental conditions and population processes at the poleward edges of breeding or non-breeding distributions (but see e.g. Job and Bednekoff 2011; Tellería 2014; Ruthrauff et al. 2018; Lavoie et al. 2021).

The northwest European breeding population of Eurasian Spoonbills (*Platalea leucorodia leucorodia*) is currently recovering from a population bottleneck caused successively by several centuries of severe human exploitation and a few years of catastrophic poisoning (de Goeij et al. 2015; Lok et al. 2013a). In the period 1990–2010, the increasing Dutch breeding population started a shift from wintering mainly in West Africa to mainly wintering in southwestern Europe (Lok et al. 2011, 2013a), a shift that materialized more slowly than what would have been optimal given the site-specific survival rates (Lok et al. 2013a,b). Nevertheless, increasingly Eurasian Spoonbills winter as far north as northern France, Belgium and The Netherlands (Werkgroep Lepelaar unpubl. data). At such latitudes, they risk severe winter weather, including Atlantic storms and cold spells (Elkins 2010).

Contributing natural history knowledge to both the population and energetic perspectives on the determination of northern range limits in migratory birds, in this report we aim to learn as much as possible from a mortality event of Eurasian Spoonbills during a cold spell in February 2021 at the northern edge of the current winter range, i.e. the province of Zeeland, The Netherlands. We monitored the fates of several individuals in two wetland areas on Schouwen-Duiveland, collected the eventual casualties and carried out post-mortem analyses of the carcasses to verify whether

they died from starvation. We recognize that starvation will not be a single cause, as factors like hypothermia (which requires the measurement of core body temperatures of live birds in the field) will have precipitated actual death.

Material and methods

Fieldwork

The fieldwork was carried out by SP on the island of Schouwen-Duiveland in the province of Zeeland, The Netherlands. The focus of the observations was a low-lying embanked area with grasslands and ponds, now a Natura 2000 wetland, next to the town of Zierikzee (Fig. 1). Poignantly, the historic name of this area is 'Levensstrijd' (which can be translated as 'life's struggle'). During the cold spell in the first 2 weeks of February 2021, Levensstrijd was visited on 6 February and daily from 9 to 17 February, with the canals near Burgh-Haamstede regularly visited too to count the number of spoonbills, record their activity, assess the presence of dead birds and determine the identity of any colour-ringed individuals. Birds were aged on the basis of bill colour and the extent of black on the tips of the outer primaries (de Boer et al. 2024).

The cold spell

The temperature and wind data during February 2021 are for the nearby city of Vlissingen and made by KNMI (Royal Dutch Meteorological Institute, De Bilt). The human wind chill factor was calculated on the basis of diurnal averages of air temperature and wind speed according to https://www.calculator.net/wind-chill-calculator.html.

Fig. 1 Map of Schouwen-Duiveland in the delta area, province of Zeeland, in the southwest of The Netherlands. The two observation areas during the cold spell in early February 2021 are indicated by the circles

Collection of victims and dissections

Winter victims were retrieved from the ice floor on 12–15 February 2021. Within a day, the bodies were stored frozen until dissections by TP and AD at NIOZ Royal Netherlands Institute for Sea Research on Texel on 4 April and 8 June 2021. External measurements followed Lok et al. (2014), and dissections followed the procedures routinely used on waders (Piersma et al. 1999, 2021). Sex was determined on the basis of the presence of either (tiny) testicles, or an ovary and oviduct on the left side of the bird. We used the fresh mass of different body components as our metric, noting that the water percentage of lean tissue is constant around an average of 69% (Piersma and van Brederode 1990). To assess the relative degrees of depletion of the different tissues, we need a comparison with birds that survives through a cold spell. In the absence of really suitable material, we made a comparison with the tissue masses of a young female spoonbill born in the Camargue, France, in spring 2022, that died from an accident at Banc d'Arguin. Mauritania, in late November 2022, and was also dissected by TP and AD (unpubl. data). Being female and a juvenile, this single currently available bird for comparison should nevertheless give fair yardstick values of what to expect in a non-starved individual. While *absolute* estimates of degrees of depletion in the different tissues should thus be taken with a grain of salt, the *relative* degrees of depletion of the different tissues should be fair representations.

Results

From 5 to 6 February 2021 average air temperatures dropped from + 5 °C to below 0 °C, with further decreases in average daily air temperature to − 5 °C on 9 February (Fig. 2). The first snow fell on 6 February at 23:00 h in the evening. For the next 5 days this level of frost was maintained, with thaw arriving on 15 February. As the frost period started, the wind picked up too, resulting in (human) wind chill temperatures dropping to below − 10 °C for 7 days in a row from 7 February. By 7 February, many freshwater ponds had started to freeze up (Fig. 3), with the Levensstrijd area already losing all open water that day. Although the strong winds lowered the wind chill temperature, they also prevented several larger waters than those at Levensstrijd area to freeze over completely.

On 6 February in the late afternoon, at Levensstrijd eight spoonbills were resting in the lee of a reedbed. They were all juvenile and included one identifiable individual with code ring NBHP. On 9 February, on 10 February (the water now completely frozen over) and on 11 February, always in the late afternoon, six juvenile spoonbills, and this included NBHP, were standing immobile in the

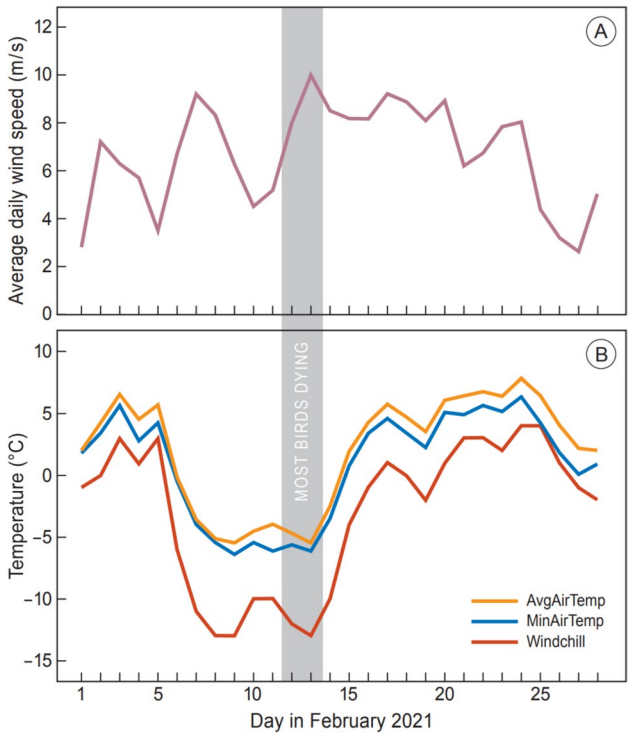

Fig. 2 Variations in the (daily average) air temperature, wind speed and calculated wind chill factor in February 2021 based on weather data from Vlissingen (KNMI)

lee of the reedbed. On 12 February, three juveniles had died at Levensstrijd. Yet, there still were six spoonbills (including NBHP), which were observed from 14:00 h to sunset at 17:45 h. Like the others, NBHP was asleep almost continuously, but remained alert to what happened around her. Upon disturbance by human skaters, she made a short flight with a radius of some 50 m. A few times she explored, with her bill, the ridges in the ice, but never walked more than a few metres. Just after sunrise on 13 February, NBHP was dead, lying with spread wings on the ice. A single live juvenile spoonbill was still around too; it seemed fit and capable of flight. Nevertheless, in the early morning of 14 February, two more juveniles were found dead at Levensstrijd, with no survivors remaining.

During the cold spell, there were spoonbills elsewhere on Schouwen-Duiveland too. On 10 February, a group of 26 birds, mostly adults with a few immatures, was observed in the open water of a canal near Burgh-Haamstede. Not all of these spoonbills seemed to have survived either, as an emaciated dead adult was found on 14 February, followed by a dead juvenile on 15 February. Of the eight collected winter victims, six juveniles came from Levensstrijd near Zierikzee and a juvenile and an adult from near Burgh-Haamstede. This included NBHP, a female born in the Ouwerkerkse Inlagen only 6.4 km from Levensstrijd as the crow flies, where she received a code ring on 7 June 2020.

With average body mass values of 1224 g (the four males) and 1111 g (the four females; Table 1), the body mass values at death were a fraction of 0.71 of the predicted asymptotic fledging mass of 1729 g in males and 0.76 of the predicted fledging mass of 1467 g in females (Lok et al. 2014). This is just a little lower than the fraction of 0.79 of the body mass of the healthy young female from Mauritania (Table 1; note that the external body dimensions of the Mauritanian female are similar to those of the winter-starved spoonbills). The dissected specimens showed no fat, their masses (and those of the organs and muscles as well) tightly correlating with body size (represented by total head length in Fig. 4). The mass fractions of the different body parts of the winter-starved spoonbills (compared to 'normal') were high for lungs (i.e. no loss; Table 1), medium for leg muscles (a loss of 20%) and low for the flight muscles and the internal organs heart, stomach, intestines and liver (losses of 40–65%).

Fig. 3 Two juvenile spoonbills resting in the lee of a narrow reedbed at Levensstrijd, Schouwen-Duiveland, The Netherlands, on 12 February 2021, with a detail of spoonbill NBHP on the day before she was found dead. Photos by SP

Table 1 Body size and composition of the eight spoonbills that died in Zeeland during a cold spell in February 2021

Variable	Females ($n=4$)			Ratio starved/normal	Males ($n=4$)		
	Average	SD	Range		Average	SD	Range
Body mass (g)	1111	44	1044–1157	0.79	1224	26	1191–1263
Total head length (mm)	228.0	10.1	215–232	1.01	253.8	6.4	245–263
Bill length (mm)	182.3	7.9	174–195	0.99	201.3	7.6	190–210
Tarsus length (mm)	131.7	8.8	118–142	1.04	144.0	1.4	143–146
Tarsus + toe length (mm)	223.8	7.2	213–232	1.02	238.8	6.8	230–248
Wing length (mm)	358.8	9.0	347–372	1.02	368.3	6.1	362–377
Flight muscles (g)	147.9	3.9	144–154	0.61	174.3	15.2	154–196
Leg muscles (g)	75.5	10.8	67–94	0.77	76.9	7.8	69–90
Heart (g)	13.7	1.6	12.4–16.4	0.55	15.0	0.8	13.8–16.1
Lungs (g)	14.8	1.7	12.4–16.6	1.23	15.6	2.9	10.7–17.5
Stomach (g)	27.4	1.2	25.5–28.5	0.58	31.0	3.5	25.5–34.2
Intestines (g)	44.5	1.3	42.4–45.8	0.46	44.8	6.5	35.7–54.0
Liver (g)	20.0	2.9	16.1–23.0	0.35	25.1	3.9	20.3–30.7
Kidneys (g)	12.6	1.2	11.4–14.5	0.66	14.0	2.0	11.4–16.7
Total organs and muscles (g)	3563	8.4	347–370		396.9	12.0	383–410

All males were juvenile (i.e. having black-tipped primaries), but one of the females was adult. Masses of organs and muscle refer to fresh mass values. The *n*-value of tarsus of males is 3. For females, the ratio between the values of the winter victims was compared with that of a healthy normal young female found freshly dead at Banc d'Arguin in Mauritania

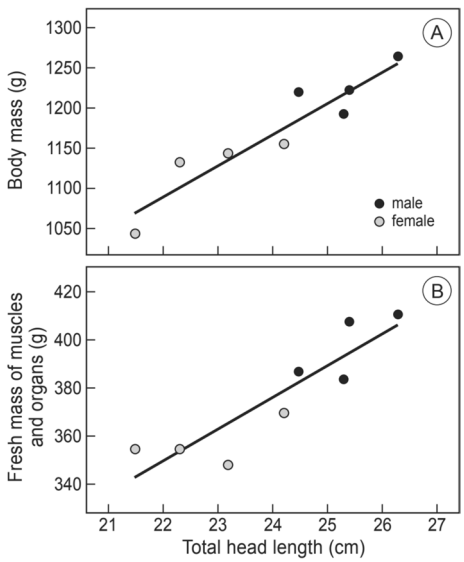

Fig. 4 The body mass at death of spoonbills dying during a cold spell in February in Zeeland was well explained by the body dimension, in this case total head length ($r=0.94$, top). This was also true for the summed fresh mass of muscles and body organs ($r=0.90$, bottom)

Discussion

Red knots (*Calidris canutus islandica*) that starved during winter cold spells in the Oosterschelde, just south of where the spoonbills died (Dietz and Piersma 2007), showed a similar degrees of body mass depletion as reported here, i.e. a fraction of 0.68 of the expected winter body mass. Eurasian Spoonbills as well as red knots appeared to best 'defend' the leg muscles during winter starvation, with internal organs like intestines and liver showing the biggest relative losses in both cases. These organs have particularly high tissue turnover (Piersma and van Gils 2011) and can thus be built up quickly in case of a timely change of weather and feeding opportunities—when the birds do need the better defended leg muscles to feed. The complete lack of fat indicates that several days before death the cold spell victims must have shifted from mainly using fat to using protein as their reserve fuel (Le Maho 1983; Cherel et al. 1988; van der Meer and Piersma 1994). As the energy density of (wet!) protein is a factor eight lower than that of fat (Jenni and Jenni-Eiermann 1998), rates of tissue loss will increase at this point. With small pectoral muscles (for shivering) and a small heart (to push blood circulation), this will diminish the capacity to generate heat, at air temperatures of −5 °C and wind speeds of 8–10 m/s leading to hypothermia and death. We suggest that actively foraging birds in the nearby flocks with access to open water, could still metabolize fat, generate heat by muscle shivering and distribute that heat by pumping blood around. It must have been the combination of starvation and diminished metabolic capacities, rather than simply the cold, that did the young birds in. Almost all the,

presumably much better fed, adults in the open water near Burgh-Haamstede survived.

This begs the question why the young birds at Levensstrijd did not start moving as soon as the open water there turned into an ice floor. They were still able to fly, and the variable numbers at Levensstrijd confirms that they were still moving around. Perhaps, the young birds were already having such low fat stores at the start of the cold spell that the physiological trigger to start moving (Robin et al. 1987; Piersma and Poot 1993) had already passed. At such low nutritional levels, one or two cold and windy days could have brought them in a metabolic state of starvation and a mental state of lethargy, a process that was earlier described for a young spoonbill carrying a GPS tracker. Called Dirkje, this spoonbill also became immobile during a cold spell and stayed put on an ice floor in a reed bed until she died (Piersma et al. 2022). On the basis of the observed movements in the months before the cold spell by youngsters like NBHP, we know that the starving birds should have been aware of alternative sites such as the site at Burgh-Haamstede, only 8 km away as the crow flies (Fig. 1). Spoonbills routinely cover such a distance during foraging trips (e.g. Lok et al. 2024) and the deceased spoonbills could still fly the day before being found dead. So, were they unable to assess the likelihood these sites still held open water? Were they thwarted by the strong winds? Or does the apparent clustering of age groups (including already prior to the cold spell) hint at subtle 'despotic' (rather than 'ideal free') processes (Parker and Sutherland 1986; Leyrer et al. 2012), with dominance relationships and anticipated aggression preventing these young spoonbills to join the flock of adults?

Despite the great interest in climate change effects on the distribution of animals (Khaliq et al. 2014; Buckley et al. 2018) and geographic range limits (Gaston 2003, 2009; Lavoie et al. 2021), the behavioural details of death under range-limiting environmental conditions appears to have received little attention. Is what we see in spoonbills, with young birds making up the bulk of the population at the northern range limits (Werkgroep Lepelaar unpubl. data; van Eerden, unpubl. data), but dying first when conditions become challenging, the general pattern? Do youngsters generally pave the way to northward expansion, at the risk of their lives being cut short by cold spells? At least in Eurasian Oystercatchers (*Haematopus ostralegus*), during cold spells the youngest individuals were also most likely to die, despite them having deposited greater winter fat stores than older birds (Zwarts et al. 1996).

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Data availability All data are presented in Table 1.

Declarations

Competing interest The authors declare no competing interests.

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Authors and Affiliations

Theunis Piersma[1,2,3] · Sven Prins[4] · Anne Dekinga[2]

✉ Theunis Piersma
Theunis.Piersma@nioz.nl

[1] BirdEyes, Centre for Global Ecological Change at the Faculties of Science & Engineering and Campus Fryslân, University of Groningen, Wirdumerdijk 34, 8911 CE Leeuwarden, The Netherlands

[2] Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands

[3] Rudi Drent Chair in Global Flyway Ecology, Groningen Institute for Evolutionary Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

[4] Bettewaardsedijk 8, 4301 PC Zierikzee, The Netherlands