

Is the resident subspecies of the Eurasian spoonbill in Mauritania, *Platalea leucorodia balsaci*, threatened by introgression of genes from the migratory nominate subspecies *leucorodia*?

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Abstract Throughout its range, the Eurasian spoonbill *Platalea leucorodia* is migratory, but there is a well-documented exception in a population living in the Parc National du Banc d'Arguin in Mauritania. Based on their smaller body size, absence of a yellowish breast band during breeding, and fully black bills, they were assigned subspecies status (*Platalea leucorodia balsaci*) in 1974. Despite obvious threats (small numbers, and their low-lying breeding islets being under pressure from sea level rise), the Mauritanian spoonbill has not been assessed for inclusion on the IUCN Red List. The nominate subspecies *P. leucorodia leucorodia*, which joins the Mauritanian subspecies at Banc d'Arguin during the non-breeding season, is categorized as Least Concern. There is genetic and behavioural evidence of gene flow between *balsaci* and *leucorodia*, and in December 2023 and 2024, we observed that over half of the spoonbills born at Banc d'Arguin (identifiable by their colour-rings) had the yellow-tipped bill characteristic of *leucorodia*. As the increase in the marked *balsaci* population has not resulted in resightings away from Banc d'Arguin in the well-monitored flyway of *leucorodia* from West Africa to Europe, the introgression of *leucorodia* genes into *balsaci* seems to have left the isolating character of residency of the Banc d'Arguin-breeding spoonbills intact. We propose that the subspecies *balsaci* should be categorized as Vulnerable on the IUCN Red List. We recommend continued monitoring of the breeding population of *balsaci*, with the inclusion of new studies of morphology and genetics.

Keywords Banc d'Arguin, bill morphology, gene flow, hybridization, introgression, IUCN Red List, *Platalea leucorodia balsaci*, seasonal migration

The Eurasian spoonbill *Platalea leucorodia* is categorized as Least Concern on the IUCN Red List as it has a wide range and a large population (BirdLife International, 2019). This foregoes the knowledge that there is at least one small, and peculiarly resident, population confined to the Parc National du Banc d'Arguin in Mauritania, which was recognized as a separate subspecies in 1974 (de Naurois & Roux, 1974; Triplet et al., 2008). It was named *Platalea leucorodia balsaci*, to distinguish it from the nominate migratory subspecies *Platalea leucorodia leucorodia*, which also occurs in the area during the non-breeding season. At the time, the impressive waterbird diversity of Banc d'Arguin had only just become known among ornithologists (de Naurois, 1959; von Westernhagen 1968, 1970).

With the type specimen collected on the islet of Zira on 8 June 1972, *balsaci* spoonbills (now called Mauritanian spoonbills) were described as being of smaller body size than *leucorodia*, with the yellowish markings on the spatulate end of the beak absent or vestigial and the ochre band at the base of the neck also absent or vestigial. Of the 17 breeding specimens collected at Banc d'Arguin during 1960–1972 (curated at MNHN, Paris), nine had completely black bill tips and eight had barely visible yellow marks. The proposed *balsaci* spoonbills were considered to be fully resident (de Naurois & Roux, 1974), but were joined during the non-breeding part of the year, and sometimes even within the Banc d'Arguin breeding season, by *leucorodia* migrants from breeding colonies in Europe (identifiable on the basis of colour-rings). Piersma et al. (2012) confirmed *leucorodia* and *balsaci* to be genetically distinct subspecies, but with evidence of gene flow from birds breeding in Europe to those breeding at Banc d'Arguin.

Evidence for gene flow was supported by regular observations of Netherlands-ringed birds with yellow-tipped bills being reproductively active at Banc d'Arguin during 2002–2010 (Piersma et al., 2012). From 2014, with the build-up of a colour-ringed *balsaci* population through the ringing efforts of the spoonbill team of the Parc National du Banc d'Arguin, TP, BL and Harry Horn began to note spoonbills with red flags (and thus ringed at Banc d'Arguin, and, by the definition of breeding location rather than morphology, belonging to *balsaci*) that had bill tip

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PLATE 1 The three bill colourations of *Platalea leucorodia balsaci* born in Banc d'Arguin, and ring combinations that include a red flag and exclude a metal ring, from left to right: black, yellow spots and yellow crescent. Photos by TO at Arel on 14 December 2023.

colours similar to those of *leucorodia*; i.e. with the distinct yellow crescent on the bottom half of the dorsal surface of the spoon.

The phenomenon of genes moving from one (sub-) species to another, initially by hybridization followed by back-crossings, is called introgression (Harrison & Larson, 2014); it may have implications for conservation when it involves rare or threatened subspecies. Although introgression may increase genetic diversity, it can also lead to the erosion of locally adapted traits (Rhymer & Simberloff, 1996; Singhal et al., 2021). Whether the introgression of *leucorodia* genes will lead to the extinction of *balsaci* depends in part on what counts as the defining traits of *balsaci*.

The 12,000 km² Parc National du Banc d'Arguin is the largest marine protected area in Africa. Half of the protected area is characterized by shallow (< 20 m deep) Atlantic waters that are bordered, on the Sahara side, by c. 450 km² of intertidal flats (Campredon, 2000; Oudman et al., 2019; El-Hacen et al., 2024). There are over 15 islands and islets (Campredon, 1987, 2000), with a few, including Nair (see below), hosting breeding colonies of Mauritanian spoonbills (Isenmann, 2006). Numbers of pairs have varied between 400 and 1,600 in recent years (Parc National du Banc d'Arguin, unpubl. data.). Notable for their isolation from depredation by land mammals, the low-lying islands are now under threat from sea level rise; high spring tides

have already destroyed colonies on several occasions (MC & EME, unpubl. data)

To reassess bill colouration in the *balsaci* spoonbills at Banc d'Arguin (i.e. to indirectly assess the degree of introgression), we used visual observations and digital photography to score bill tip colouration in colour-ringed individuals of known origin. During 14–15 December 2023 and 1–3 December 2024, we made observations at the high tide roosts of Arel and Nair (El-Hacen et al., 2013). Arel (centred at 19°53'54"N, 16°30'08"W) is the most remote, a rocky outcrop of a few ha surrounded by seagrass-covered intertidal flats. It lies 20 km from the mainland and provides a high tide roost for up to 6,000 spoonbills (Altenburg et al., 1982; TP & MC, unpubl. data). Nair (centred at 19°51'36"N, 16°24'35"W) is a low, sandy island a little larger than Arel, but only 8 km offshore. It offers high tide roosting space for up to 2,000 spoonbills.

In 178 individually colour-ringed adults (Table 1), we assigned the colour of the tip of the upper mandible to one of three categories: completely black, with yellow spots or with a yellow crescent (Plate 1). The young of the year and even some 1-year old birds show uniform light, pinkish colouration across the bill. The assignment of the three categories appeared robust for 36 adults that were observed multiple times, in most cases by multiple observers, at Arel or Nair during 1–3 December 2024; only five (14%) were assigned to adjacent categories on different occasions;

TABLE 1 Scores of the colour of the upper surface of the bill tips of Eurasian spoonbills *Platalea leucorodia* in 2023 and 2024, for which the breeding origin is indicated by their individual colour-ring combination. Spoonbills born and colour-ringed in Europe (with one bird born and colour-ringed in Morocco scored in 2024) are supposed to represent the subspecies *Platalea leucorodia leucorodia*, whereas birds born in Mauritania belong to the subspecies *Platalea leucorodia balsaci*.

Year	Colouration of the upper bill tip			Total (%)
	Number black (%)	Number with yellow spots (%)	Number with yellow crescent (%)	
Colour-ringed in Europe				
2023		1 (14)	6 (86)	7 (100)
2024		1 (2)	45 (98)	46 (100)
Total		2 (4)	51 (96)	53 (100)
Colour-ringed in Mauritania				
2023	12 (30)	11 (28)	17 (42)	40 (100)
2024	19 (22)	16 (19)	50 (59)	85 (100)
Total	31 (25)	27 (22)	67 (53)	125 (100)

i.e. they were classified as having yellow spots by some observers, and either a completely black tip or a yellow crescent by others. For the 36 adults observed multiple times, there were mostly three or more independent observations (i.e. on different days and/or by different observers), and the category that was ultimately assigned was decided by the majority of observer votes. In one case, there were only two independent observations (one recording a black bill tip and one yellow spots); we assigned this individual to the yellow spots category. Because of the time of the year, we only examined non-breeders, so we were unable to assess the presence (*leucorodia*) or absence (*balsaci*) of the ochre breast band. Neither were we able to assess body size (it needs capture or collection), although several observers noted that some red-flagged (*balsaci*) individuals appeared large.

Confirming the known morphology of *leucorodia* spoonbills, almost all birds of European origin had yellowish crescents on the bill tips, with only two of 53 having yellow spots (Table 1). We also confirmed the suggestion that many *balsaci* have *leucorodia*-type bills, with > 50% of the individuals born and ringed at Banc d'Arguin having yellow crescents, and 22% having yellow spots (Table 1). Only 25% of the Banc d'Arguin-born birds now have the typical fully black bills. It remains to be seen whether the increase in the proportion of Banc d'Arguin-born birds having yellow crescents, from 42% in 2023 to 59% in 2024 (Table 1), is a continuing trend.

In January–February 1980, on the basis of bill colouration, Altenburg et al. (1982) categorized 1,652 spoonbills individually assessed at Arel and at Zira as either black-tipped *balsaci* (93%) or yellow-tipped *leucorodia* (7%). With a total winter population at Banc d'Arguin of c. 9,000 non-breeding spoonbills, this suggested that in the winter of 1979–1980 there were c. 8,000 *balsaci* and c. 1,000 wintering *leucorodia* at Banc d'Arguin. This was when the European

breeding population of *leucorodia* was only c. 600 breeding pairs (de Goeij et al., 2015). During the six complete waterbird counts at Banc d'Arguin during 1997–2017, the total numbers of spoonbills never exceeded (and was never far below) 9,000 individuals (Oudman et al., 2019), even though the European population meanwhile increased to c. 6,000 pairs (de Goeij et al., 2015; PdG et al., unpubl. data). Although in 1980 over half of the Dutch breeding spoonbills were estimated to winter in West Africa, this had dropped by 50% in 2010 (Lok et al., 2011, 2013a), with the proportion declining further since (A.O.K. van Eerden & T. Lok, unpubl. data). The breeding and crossbreeding of *leucorodia* birds born in Europe at Banc d'Arguin recorded from 1981 onwards thus coincided with a marked increase in the size of the *leucorodia* breeding population, even if the proportion migrating to West Africa began to fall steeply. Not only did density-dependent forces explain the declining late-winter survival at increasing European breeding population sizes (Lok et al., 2011, 2013b), the population pressure may also have pushed individuals to remain at Banc d'Arguin and hybridize with *balsaci*.

Despite the evidence of Netherlands-born *leucorodia* spoonbills being reproductively active at Banc d'Arguin, Mauritania-born birds have not been recorded in breeding colonies in Europe (but there is movement of individuals within Europe). The large and growing observer effort along the flyway (e.g. Piersma et al., 2022), has not yielded any resightings of red-flagged individuals in western Europe that would indicate Mauritania-born spoonbills are migrating north. This suggests that, although introgression of *leucorodia* genes into the *balsaci* population has led to changes at least in bill morphology, it has not affected a key behavioural characteristic of the Banc d'Arguin population; i.e. their residency. The absence of evidence of migratory behaviour in the now heavily hybridized *balsaci* is consistent with the idea that seasonal migration is primarily a

cultural phenomenon (Piersma, 2024) that is based on learning by naïve youngsters, including social learning from more experienced older birds (godwits *Limosa lapponica*: Loonstra et al., 2023; spoonbills: A.O.K. van Eerden et al., unpubl. data). It is possible that migratory behaviour could develop post-fledging, or never develop at all. With most *leucorodia* still in Europe when the young *balsaci* fledge in summer, this would prevent *balsaci* youngsters learning from *leucorodia*.

If year-long residency and an absence of seasonal migration are considered key traits, *balsaci* is still a valid subspecies (see Bom et al., 2022 for a similar discussion about a shorebird). Residency will continue to serve the breeding population with a degree of isolation, with the potential for local adaptation and the possibility of *balsaci* regaining genetic distinctiveness if seasonal pressures on the migrant *leucorodia* population changes and introgression diminishes. Nevertheless, it seems an oversight not to assess Mauritanian spoonbills *P. leucorodia balsaci* for the IUCN Red List. In addition to the threats listed by Triplet et al. (2008), introgression is now a concern.

We propose that the *balsaci* subspecies should be categorized as Vulnerable based on criteria B1a,C1: extent of occurrence < 20,000 km² (B1) and limited to a single location, the Parc National du Banc d'Arguin (a); and population < 10,000 mature individuals (C), with the likelihood of at least a 10% reduction in three generations (1) because of reliance on low-lying breeding islets that are threatened by sea level rise.

To summarize, despite the serious introgression of *leucorodia* genes into *balsaci* that the documented change in bill morphology suggests, residency as a character of the Banc d'Arguin-breeding spoonbills appears intact. Nevertheless, there is a need for conservation attention. We recommend assessment of the subspecies *balsaci* on the IUCN Red List as Vulnerable, and continued monitoring, by the Parc National du Banc d'Arguin and partners, of the breeding population of *balsaci*, with the inclusion of studies on morphology and genetics.

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Ethical standards No specific approval other than a research permit from the Parc National du Banc d'Arguin was required to conduct this non-invasive observational work.

Data availability All data discussed are presented within the article.

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