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# Evidence of distribution overlap between Atlantic and Baltic grey seals

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## Abstract

Grey seals from both the Atlantic and Baltic Sea subspecies are recovering from dramatic declines and recolonising former ranges, potentially leading to overlapping distributions and an emerging subspecies transition zone in Kattegat between Denmark and Sweden. The two subspecies have asynchronous moulting and pupping seasons. We present aerial survey data from 2011 to 2023 in Danish Kattegat during the Atlantic subspecies' moulting (March–April) and pupping (December–January) seasons, as well as the Baltic subspecies' moulting season (May–June). During the Atlantic subspecies' peak moulting season, 82% of the grey seals were recorded north of the island of Læsø (N57°18', E11°00'). In contrast, during the Baltic moulting season in those years, only 9% of the grey seals were recorded here. This indicates a predominance of Atlantic grey seals in the north and Baltic grey seals in central and southern Kattegat. In 2022 and 2023, three pups were recorded around Læsø during early January, which coincides with the pupping season of northern Wadden Sea grey seals. Previously, pups have been recorded in the same locations during the Baltic pupping season, which demonstrates overlapping breeding ranges. Grey seals are known to have plasticity in the timing of pupping indicated by a west to east cline of progressively later pupping in the eastern North Atlantic. Historical sources document that the Baltic pupping season in Kattegat was earlier than it has been in recent years. Thus, the expanding ranges may be associated with convergence of Atlantic and Baltic subspecies' pupping seasons and potential hybridisation in this emerging transition zone.

## Introduction

The grey seal (*Halichoerus grypus*) is a North Atlantic phocid seal, ranging from the north-eastern United States and the Canadian Maritimes in the west to the Kola Peninsula of Russia and the Baltic Sea in the east. Two distinct subspecies are currently recognised, one in the North Atlantic Ocean (*H. g. atlantica*) and one in the Baltic Sea (*H. g. grypus*), which are characterised by genetic and phenotypic differences (Heptner *et al.*, 1976; Berta and Churchill, 2012; Fietz *et al.*, 2016; Olsen *et al.*, 2016), although Galatius *et al.* (2022) found negligible differences in skull shape. In Europe, the subspecies differences are most apparent in terms of pupping and moulting seasons, which for the Atlantic subspecies in the eastern North Sea region occur from December to January and March to April (Brasseur *et al.*, 2015; Schop *et al.*, 2017), while the Baltic subspecies pups and moults in February–March and May–June, respectively (Hook and Johnels, 1972; Jüssi *et al.*, 2008; Galatius *et al.*, 2014).

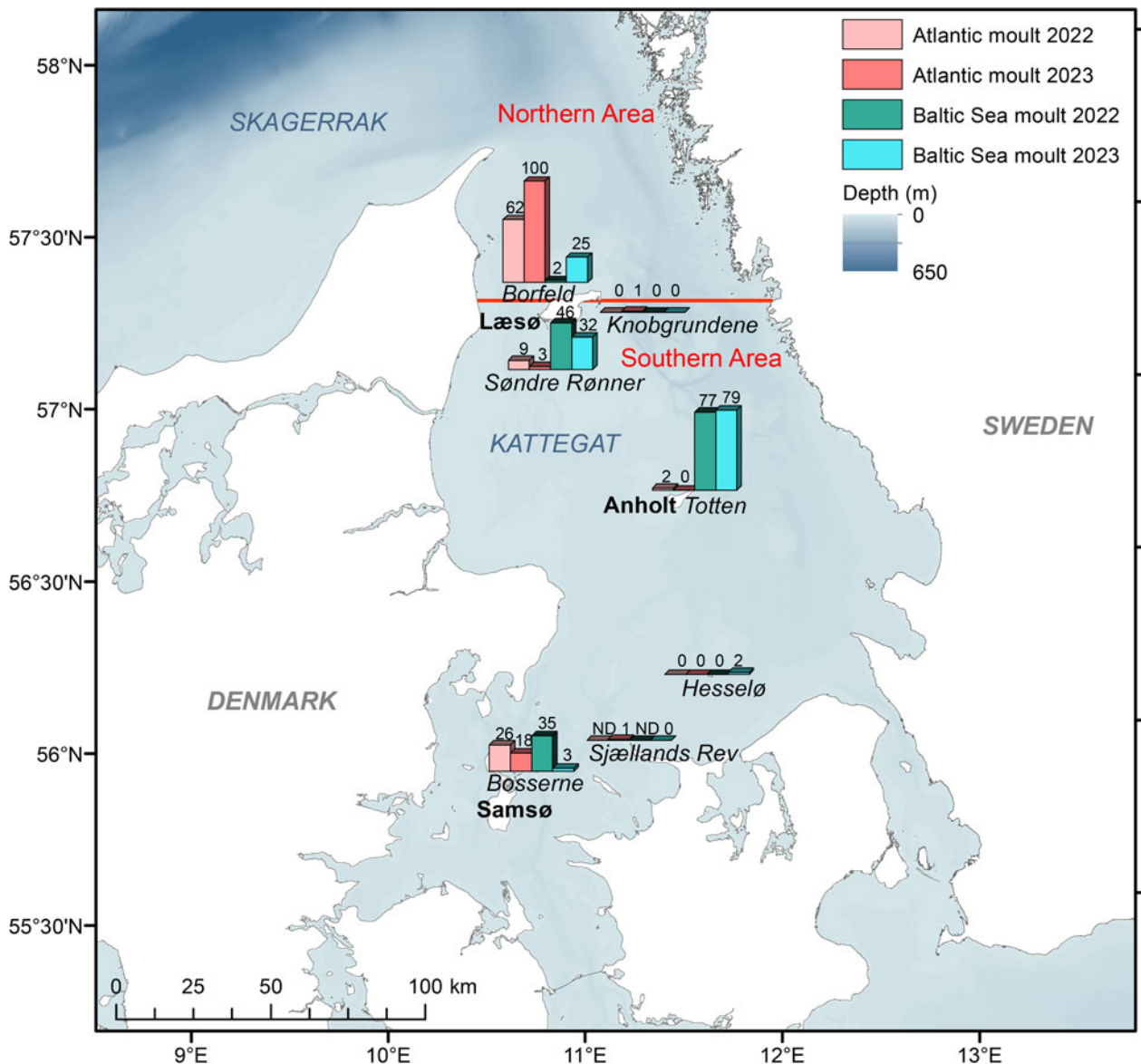
The grey seal was historically abundant along the coasts of continental Europe, but apart from the Norwegian west coast and the Baltic Sea, the species disappeared from the European mainland during the 16th century (Reijnders *et al.*, 1995; Härkönen *et al.*, 2007). Later, Atlantic grey seals were also hunted to a very low numbers in the United Kingdom, where they were estimated to have an abundance of 500 individuals in 1914 (Lambert, 2002; Lonergan *et al.*, 2011). This low estimate led to the protection of the species in the United Kingdom, and the population began growing at annual rates of 6–7%, leading to an estimated abundance of 70,000 seals in the 1970s (Summers, 1978). In the 1950s, individuals started appearing in the German and Dutch Wadden Sea, and in the 1980s, grey seals were breeding regularly at a few localities here (Scheibel and Weidel, 1988; Reijnders *et al.*, 1995). Since then, grey seal occurrence and breeding activity has grown at high annual rates in the Wadden Sea area (19% for pup counts in the Netherlands), fuelled by immigration from the United Kingdom (Brasseur *et al.*, 2015). In 2020, 1921 pups were counted at the peak of the pupping season in the Wadden Sea area and Helgoland, Germany, and during the 2022 moulting season, 8948 grey seals were counted (Schop *et al.*, 2022). During this period of growth and recolonisation, the first grey seal pup was recorded in the Danish Wadden Sea in 2014 (Jensen *et al.*, 2015). In the Baltic Sea, the Baltic subspecies experienced substantial declines due to 19th and 20th century hunting and 20th century contaminants, yet persisted at a population size in the low thousands (Härkönen *et al.*, 2007), and has since recovered to ca 40,000 animals counted on land during moulting across Sweden, Finland, Estonia, Poland, Germany and Denmark (ICES, 2022).

Kattegat, the sea area between northern Denmark and the west coast of Sweden (Figure 1), is becoming a transition zone between the Baltic and Atlantic grey seals subspecies. In this region, grey seals were abundant during prehistoric times, but became extinct as a breeding stock in the late 19th century as a result of hunting and a bounty campaign (Härkönen *et al.*, 2007; Olsen *et al.*, 2018). Fietz *et al.* (2016) used historical mitochondrial DNA analyses to document that the majority of specimens killed in Kattegat during the 19th century bounty hunt were genetically assigned to the Baltic subspecies, while contemporary grey seal hair and tissue samples from Kattegat predominantly were genetically assigned to the Atlantic subspecies. In the 1970s, when systematic surveys of harbour seals were initiated in Kattegat, counts of grey seals in the Danish region were usually in the 20s and restricted to the island of Anholt (Figure 1), and counts remained at this low level until the early 2000s (Härkönen *et al.*, 2007). Recent survey data show that grey seals have increased in abundance in Kattegat and are also present at haul-outs around the islands of Samsø and Læsø (Figure 1), where newborn pups have been recorded during the Baltic grey seal breeding season (Galatius *et al.*, 2020).

Anecdotally, a couple of observations of breeding attempts have been made, both along the Swedish west coast and in Danish Kattegat (Härkönen *et al.*, 2007), however, to date, there have not been systematic surveys of Kattegat pups or moulting grey seals during the Atlantic grey seal breeding season in late fall and early winter. To address this knowledge gap, monitoring of Danish Kattegat haul-out localities during the Atlantic grey seal breeding and moulting seasons was initiated in December 2021. Here, we use the results of the first two years of this programme, as well as data from the corresponding programme for Baltic grey seals in the region to evaluate occurrence, distribution and pupping activity in the Kattegat transition zone between the two grey seal subspecies.

## Materials and methods

The phenology of grey seal pupping and moulting seasons shows some plasticity, in particular in the Atlantic subspecies (Bowen *et al.*, 2020; Bull *et al.*, 2021; SCOS, 2022). Thus, surveys of the Kattegat were timed to best capture the current Atlantic and the Baltic pupping and moulting seasons, with some input from



**Figure 1.** Map of the study area. The grey seal counts during the Atlantic Ocean (red bars; early April) and Baltic Sea moulting seasons (blue-green bars; late May) for each haul-out in 2022 and 2023 are shown. ND, not determined, count not conducted.

	December	January	February	March	April	May	June
	Atlantic pupping			Atlantic moulting			
			Baltic pupping			Baltic moulting	
2011							
2012							
2013							
2014							
2015							
2016							
2017							
2018							
2019							
2020							
2021							
2022							
2023							

**Figure 2.** Presumed pupping and moulting seasons of Atlantic and Baltic grey seals in the study area. Survey dates for the study are marked with black bars.

historical sources (Bynch, 1801) (Figure 2; Supplementary Table 1). We first focus on data from 2022 to 2023, which represent the first two years of aerial surveys of grey seals in Danish Kattegat during the expected Atlantic subspecies pupping (December–January; two surveys per year) and moulting season (March–April; one survey) in the area. These surveys were timed according to data from the Dutch and German Wadden Sea, with pupping observed to mainly occur in mid-December and moulting observed to peak in April (Abt and Koch, 2000; Brasseur *et al.*, 2015; Schop *et al.*, 2017, 2022). Yet, to also take into account data from the Danish Wadden Sea, where all of the six newborn grey seal pups recorded since 2014 were observed between 28 December and 4 January (Sveegaard *et al.*, 2023), one of the seasonal pupping surveys in Kattegat was conducted in mid-December (to reflect the peak pupping season in the larger Wadden Sea) and one in early January (to reflect pupping in the Danish Wadden Sea). Second, to assess longer time-series trends in Kattegat grey seal abundance, we present data collected in Kattegat since 2011 during the Baltic subspecies moulting (late May–early June) and late pupping seasons (mid-March), the latter period corresponding to the early moulting period of Atlantic grey seals in the Wadden Sea.

Aerial surveys covered all grey seal haul-outs known from historical sources (Bynch, 1801; Faber, 1828; Søndergaard *et al.*, 1976), harbour seal monitoring and anecdotal observations in the Danish part of Kattegat, except Bosserne, which was added as a survey site in 2017 after grey seals were recorded here. The haul-outs are named on the Figure 1 map. Surveys were conducted at wind speeds below  $10 \text{ m s}^{-1}$  and without precipitation at any locality in the preceding 6 h. All localities were surveyed between 8:00 and 17:00 local time. As tides are negligible in Kattegat, surveys were not timed in relation to these. Two observers both took overlapping photographs using DSLR cameras with 80–200 mm lenses from the same side of the plane of all groups of seals observed through an open window in a single-engine Cessna 172 or 182, flying at 500–600 feet over the haul-out sites. The haul-out at the Knobgrundene sand bank where seals are prone to flushing was overflowed at 1000 feet. The digital photographs were subsequently used to count the number of seals present by two independent observers. If the counts for a location differed by more than 5% between the two observers, a third (or more) count(s) was performed until there was agreement between the counts.

## Results and discussion

### Moulting season

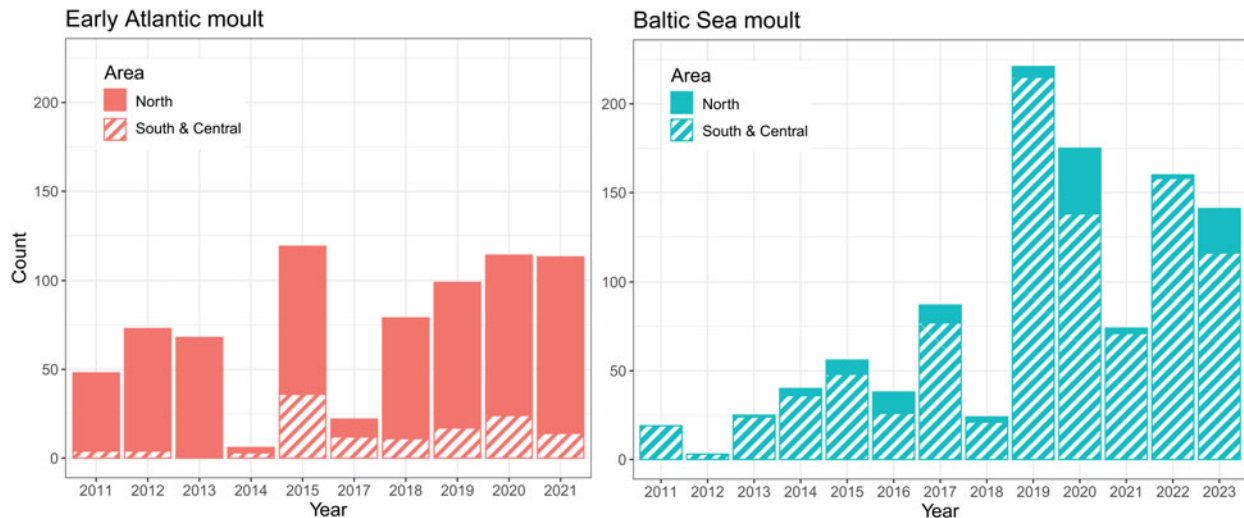
In both 2022 and 2023, the counts of hauled out grey seals in Danish Kattegat during the Atlantic grey seal moulting seasons

and those during the Baltic moulting seasons were largely similar, all ranging between 99 and 160 grey seals (Figure 1). However, while the total counts were similar, the geographic distributions of the counts differed between the two seasons; during the Atlantic moulting season, the majority of grey seals were recorded at the Borfeld haul-out north of Læsø Island, while during the Baltic moulting season counts, the majority of grey seals were counted at haul-out sites south of Læsø, including Sønder Rønner skerries and the island of Anholt and Bosserne sand bar.

The observed pattern of partitioning is corroborated by previous counts since 2011 that were conducted during the Baltic pupping season in March and the moulting season in May–June (Figure 3). In the March counts, which overlap with the early Atlantic moulting season, most grey seals were counted north of Læsø, while counts from May to June were dominated by seals in the central and southern areas south of Læsø and around Anholt and Samsø. This indicates that in the Kattegat transition area between the two subspecies, Atlantic grey seals were predominant in the northern part of Kattegat, while Baltic Sea grey seals were most abundant in the central and southern parts. This fits well with the observations by Fietz *et al.* (2016), where most of the contemporary hair and tissue samples collected in Kattegat were from Borfeld at Læsø and genetically assigned to the Atlantic subspecies. Given the lack of contemporary samples from other Kattegat sites, this may have led Fietz *et al.* (2016) to overestimate the relative occurrence of Atlantic grey seals in Kattegat, in light of the monitoring data presented here.

The current moult counts of around 100 grey seals in Kattegat contrasts markedly with the historical dominance of grey seals relative to harbour seals in the region (Søndergaard *et al.*, 1976; Olsen *et al.*, 2018) and are dwarfed by contemporary moult counts of harbour seals in August, which have ranged from 8000 to 9000 seals between 2010 and 2021 (Silva *et al.*, 2021). This implies that grey seal recolonisation of Kattegat is still in an early stage, yet the survey data presented here indicate that grey seal presence is increasing, particularly in the southern and central parts of Kattegat during the Baltic moulting season (Figure 3). In other areas, e.g. Southeast UK, harbour seal populations have declined when grey seal populations have increased, although no causality linking the contrasting population trajectories has been established (SCOS, 2022). As grey seal and harbour seal diets may overlap in areas where both species occur (Wilson and Hammond, 2016; Scharff-Olsen *et al.*, 2019), it is likely that there will be direct competition between the species. Furthermore, grey seal predation on harbour seals has been documented since 10 years ago in the North Sea (van Neer *et al.*, 2015) and recently in the Baltic Sea (Westphal *et al.*, 2023). Increasing





**Figure 3.** Counts of grey seals in Danish Kattegat during the early Atlantic moulting season in mid-March and the peak Baltic moulting season in late May and early June. Years with no data are not shown. Bars are colour-coded according to season (Atlantic moult: red; Baltic moult: blue-green) and counts in northern Kattegat at Borfeld Reef north of Læsø are in solid colour while counts in southern and central Kattegat at haul-out sites south of Læsø Island and around Samsø, Hesselø and Anholt islands are hatched.

overlap and contact between the two subspecies may facilitate the transmission of this phenomenon.

In the Swedish Kattegat region, seal surveys are not conducted during the grey seal moulting or pupping seasons. However, based on surveys targeting moulting harbour seals in August, grey seals are scarce in this region, averaging between 3 and 17 animals per year along the entire western Swedish coastline in the years 2015–2021 (M. Ahola, Swedish Museum of Natural History, pers. comm.). The corresponding numbers for the Danish part of Kattegat in August range between 23 and 47 grey seals in this period (data not shown).

#### Pupping season

During our pupping surveys in Kattegat in December–January, we recorded two grey seal pups in the season 2021/2022 (one at

Søndre Rønner and the other at Borfeld) and one in 2022/2023 (at Borfeld) around Læsø Island in northern Kattegat (Figure 4). Based on the photos, all three pups were at developmental stage 2 (Jenssen *et al.*, 2010), with an estimated age of 4–12 days. This documents the emerging overlap of the breeding ranges of the grey seal subspecies, as there is also breeding activity at these haul-outs during the Baltic grey seal pupping season in late February to mid-March (Galatius *et al.*, 2020; Supplementary Table 1). The few observations of pups are concordant with other studies of grey seal recolonisation of their former range, where pupping activity lags behind occurrence during the moulting season and other parts of the year (Brasseur *et al.*, 2015; Galatius *et al.*, 2020; Wood *et al.*, 2020).

All three grey seal pups in Kattegat were recorded in early January, two on 6 January 2022 and one on 4 January 2023. This is consistent with data from the Danish Wadden Sea,



**Figure 4.** Survey photograph of grey seal mother and pup at Borfeld Reef, Kattegat on 6 January 2022. The two animals are highlighted by a white rectangle.

where all six pups detected between 2014 and 2021 were found between 28 December and 4 January (Sveegaard *et al.*, 2023), but late compared to the pupping season in the general Wadden Sea area, which occurs between mid-November and December (Abt and Koch, 2000; Brasseur *et al.*, 2015). The late parturitions in both the Danish Wadden Sea and Kattegat may be because immigrating breeding females are young, as younger female grey seals are known to pup later than older females (Bowen *et al.*, 2020; Bull *et al.*, 2021). It has also been observed that pupping may shift earlier as a colony grows (Coulson, 1981). However, the late pupping may also be related to a geographical trend of gradually later pupping times. There is a clockwise sequential cline in pupping date around the UK, with the earliest being Southwest England and Wales, where the pupping season begins in August (Bull *et al.*, 2021). The cline proceeds from Wales through West Scotland, Shetland, Orkney, East Scotland and finally Southeast England in November–December (SCOS, 2022). Although recent studies cast doubt on the link between sea temperature and the timing of grey seal pupping, at least within local areas (Bowen *et al.*, 2020; Bull *et al.*, 2021), this pattern is tightly linked with observed mean winter sea surface temperatures from the World Ocean Atlas (Locarnini *et al.*, 2019).

If the trend of gradually later pupping dates with decreasing winter sea temperature is extrapolated into our study region, it suggests the possibility that the pupping seasons of Atlantic and Baltic grey seal subspecies may start to overlap once the Kattegat transition zone is further colonised from both the warmer North Atlantic and colder Baltic Sea. Indeed, historical sources indicate that Kattegat pupping season fell between the current North Sea and Baltic seasons. For instance, in a detailed contemporary description of the grey seal pup catch for seal oil at Anholt in Kattegat, Bynch (1801) reported that pups sufficiently fat for capture were killed at Candlemas (2 February). Thus, at this date, many pups must have been near weaning. Based on genetic data, grey seals in Kattegat in the 19th century were of Baltic origin (Fietz *et al.*, 2016), so this implies a much earlier historic pupping season than currently in the Baltic, where pupping peaks in late February to mid-March.

The Baltic grey seal pupping period in February–March is considered an adaptation to ice breeding. For much of the 20th century, pupping on land in the Baltic was generally not documented (Hook and Johnels, 1972), however, during this historic period, Baltic grey seals were extinct in areas without ice cover during winter, potentially obscuring a gradient within the Baltic. While it could be rare cases of very late breeding Atlantic grey seal females, our observation of two newborn pups at Borfeld during an opportunistic survey on 26 January 2021 may be an early sign of a phenological adaptation to ice-free circumstances or warmer sea temperatures, potentially bridging the temporal gap between Atlantic and Baltic Sea pupping seasons.

## Conclusion and perspectives

There is already genetic evidence of hybridisation between the two subspecies in the western Baltic (Fietz *et al.*, 2016). The increasing spatial overlap and potential converging moulting and breeding phenology will facilitate further hybridisation between Atlantic and Baltic grey seal subspecies in the transition area in Kattegat. If the breeding seasons of grey seal subspecies converge in Kattegat, current genetic differences may erode over time in this transition area. A continuous range of grey seals in the eastern North Atlantic and Baltic Sea may also increase the potential for pathogen transfer. Also, a decline in the numbers of harbour seals in the recolonised areas may be seen as observed in UK waters (see above). Further knowledge on how Atlantic grey seals use the area, potential relationships to other parts of

the range of this subspecies, and possible subspecies hybridisations could be gained by tagging and collecting DNA biopsies from pups born in Kattegat, as well as older seals visiting the area.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0025315424000213>

**Data availability statement.** The data that support this study are available in Supplementary Table 1.

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**Author contributions.** A. G. designed the study. A. G., M. A.-L., J. D. B. and L. A. K. led the surveys. A. G. and S. S. analysed the data. A. G., J. T. and M. T. O. interpreted the findings. A. G. wrote the draft article. All authors edited and approved of the final draft.

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**Competing interest.** None.

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