BIOLOGICAL REVIEWS
Cambridge Philosophical Society

Biol. Rev. (2024), **99**, pp. 1717–1735.
doi: 10.1111/brv.13089

Social interactions and information use by foraging seabirds

Samantha Anne Monier[1,2,*]

[1]*Biology Department, The Graduate Center, City University of New York, 365 5th Avenue, New York, NY 10016, USA*
[2]*Biology Department, College of Staten Island, 2800 Victory Blvd., Staten Island, NY 10314, USA*

ABSTRACT

What do seabirds perceive about the world? How do they do so? And how do they use the information available to them to make foraging decisions? Social cues provide seabirds with information about the location of prey. This can, of course, be passive and not involve higher-order cognitive processes (e.g. simple conspecific or heterospecific attraction). However, seabirds display many behaviours that promote learning and the transmission of information between individuals: the vast majority of seabirds are colonial living, have an extended juvenile phase that affords them time to learn, routinely form intra- and interspecific associations, and can flexibly deploy a combination of foraging tactics. It is worth evaluating their foraging interactions in light of this. This review describes how seabirds use social information both at the colony and at sea to forage, and discusses the variation that exists both across species and amongst individuals. It is clear that social interactions are a critical and beneficial component of seabird foraging, with most of the variation concerning the way and extent to which social information is used, rather than whether it is used. While it may seem counterintuitive that large groups of potential competitors congregating at a patch can result in foraging gains, such aggregations can alter species dynamics in ways that promote coexistence. This review explores how competitive interference at a patch can be mitigated by behavioural modifications and niche segregation. Utilising others for foraging success (e.g. *via* social cues and facilitation at a patch) is likely to make population declines particularly damaging to seabirds if the quantity or quality of their social foraging interactions is reduced. Environmental changes have the potential to disrupt their social networks and thus, how these species obtain food and transfer information.

Key words: cognitive ecology, conservation, foraging, interspecific interactions, local enhancement, marine mammals, seabirds, social behaviours.

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* Author for correspondence (Tel.: +19179028881; E-mail: monier.samantha@gmail.com.

I. INTRODUCTION

As suggested by Seppänen *et al.* (2007), in what was perhaps the first review of cross-species social information use, and by many others since (Weimerskirch *et al.*, 2010; Saavedra *et al.*, 2011; McInnes *et al.*, 2017; Veit & Harrison, 2017; Monier, Veit & Manne, 2020), reliance on others for foraging success places social foragers disproportionately at risk to declines in biodiversity. This has been demonstrated in modelling studies which show that the effectiveness of a forager using social cues to find food is dependent on the presence of relatively high densities of other foragers (Boyd *et al.*, 2016; Bastos *et al.*, 2020). The weakening of mutualistic relationships can even lead to abrupt community collapse (Dakos & Bascompte, 2014). Of immediate concern is that anthropogenic changes may be disrupting social networks and thus, how animals obtain and transfer crucial information related to foraging and, by extension, individual fitness. The extent to which these species are able to adapt to changing environmental conditions likely depends on the extent to which they are reliant on social foraging tactics or can flexibly deploy other strategies. Such assessments require an understanding of a species' sensory and cognitive capabilities: what do they perceive about the world? How do they do so? And how do they use this information to make foraging decisions?

Seabirds exhibit many behaviours that promote learning and the transmission of information between individuals. First, seabirds routinely form inter- and intraspecific associations. The vast majority of seabirds nest in colonies, interacting with potentially thousands of individuals on a daily basis, but also repeatedly year after year [an estimated 98% of seabirds nest in colonies according to Wittenberger & Hunt Jr (1985); see examples in Burger, 1997; Weimerskirch *et al.*, 2010; Wakefield *et al.*, 2013; Thiebault *et al.*, 2014*a*; Sutton *et al.*, 2017; Jones *et al.*, 2018]. When foraging at sea, seabirds readily join feeding aggregations that can range in size from just a few individuals to over one million birds, marine mammals, and predatory fish (Hoffman, Heinemann & Wiens, 1981; Briggs *et al.*, 1987; Harrison *et al.*, 1991; Veit & Hunt Jr, 1991; Camphuysen & Webb, 1999; Silverman, Veit & Nevitt, 2004; Anguita & Simeone, 2016; McInnes *et al.*, 2017; McInnes & Pistorius, 2019).

Secondly, seabirds have an extended juvenile phase. Recruitment generally occurs between the ages of 2 and 9 years (Weimerskirch, 2002), although in some species, such as albatrosses, it is not uncommon for breeding to start at 10 years or later (Weimerskirch, Clobert & Jouventin, 1987; Fay *et al.*, 2016). This delayed breeding provides time for learning to occur before sexual maturity is reached (MacLean, 1986; Riotte-lambert & Weimerskirch, 2013; Grecian *et al.*, 2018). Third, seabirds have long lifespans [including the world's oldest known wild bird, a Laysan albatross (*Phoebastria immutabilis*), who was ringed as an adult in 1956 and hatched a chick as recently as 2021 (Plissner, 2021)]. Long lifespans coupled with an extended juvenile phase provides an opportunity for young (i.e. naive) seabirds to learn from adults (Yoda *et al.*, 2011; Wakefield *et al.*, 2019) and on their own through the process of exploration (Baker, 1980; Votier *et al.*, 2017; Collet *et al.*, 2020; Fayet, 2020).

The location of productive areas where prey are likely to be found is often predictable at large and meso scales (>100 km) and so can be learned. However, after arriving at a productive area, seabirds must adjust their search behaviour to locate individual prey patches, which are often mobile and can be ephemeral (Weimerskirch *et al.*, 2007; Regular, Hedd & Montevecchi, 2013). Because prey predictability varies temporally and is scale dependent, the flexible use of various search strategies should be advantageous; seabirds use various mechanisms to locate prey, both directly and indirectly (Fig. 1; Table 1). Taken together, these traits provide a potential pathway for cultural transmission among members of a given colony, regarding when, where, and how to forage (Grémillet *et al.*, 2004; Wakefield *et al.*, 2013, 2019; Sanchez *et al.*, 2018; Aplin, 2019).

Marine predators today face multifaceted stressors from changing climate to changing prey availability, and these changes are occurring at unprecedented speeds (Loeb *et al.*, 1997; Fraser & Hofmann, 2003; Atkinson *et al.*, 2004; Flores *et al.*, 2012; Paleczny *et al.*, 2015; Sydeman *et al.*, 2015*b*; Poloczanska *et al.*, 2016; Grémillet *et al.*, 2018). Changes to the birds' physical environments are likely to change the birds' social environments *via* community change. Strikingly, between 1950 and 2010, the world's monitored seabird population has decreased by nearly 70% (Paleczny *et al.*, 2015).

II. SCOPE

This review synthesises information on how seabirds use cues from, and interact with, others while foraging at sea. Seabirds regularly interact with flying birds, swimming birds such as penguins, predatory fishes such as tuna, cetaceans, and pinnipeds, all of which can provide cues to prey availability. This topic is discussed in the context of seabird sensory capabilities and any associated cognitive behaviours (i.e. what do these species perceive about the world and how do they use this information to make foraging decisions?). The memory, visual, auditory, and olfactory capabilities of seabirds are implicit in this discussion of social foraging as individuals must either remember, see, hear, or smell one another in order to make use of social information. Additionally, when birds choose to deploy social *versus* asocial search tactics is of interest. The intention of this review is not to review seabird sensory or cognitive capabilities in their entirety, but in so far as they are important to social foraging (see Fig. 1 and Table 1 for an overview), alongside the costs and benefits of social information use.

Sociality is a continuum that ranges from solitary to cooperative breeding and eusociality. There is little evidence to suggest that seabirds meet the criteria for higher levels of sociality (they do not generally have generational overlap within a family unit, breed cooperatively, or display divisions of labour). Nonetheless,

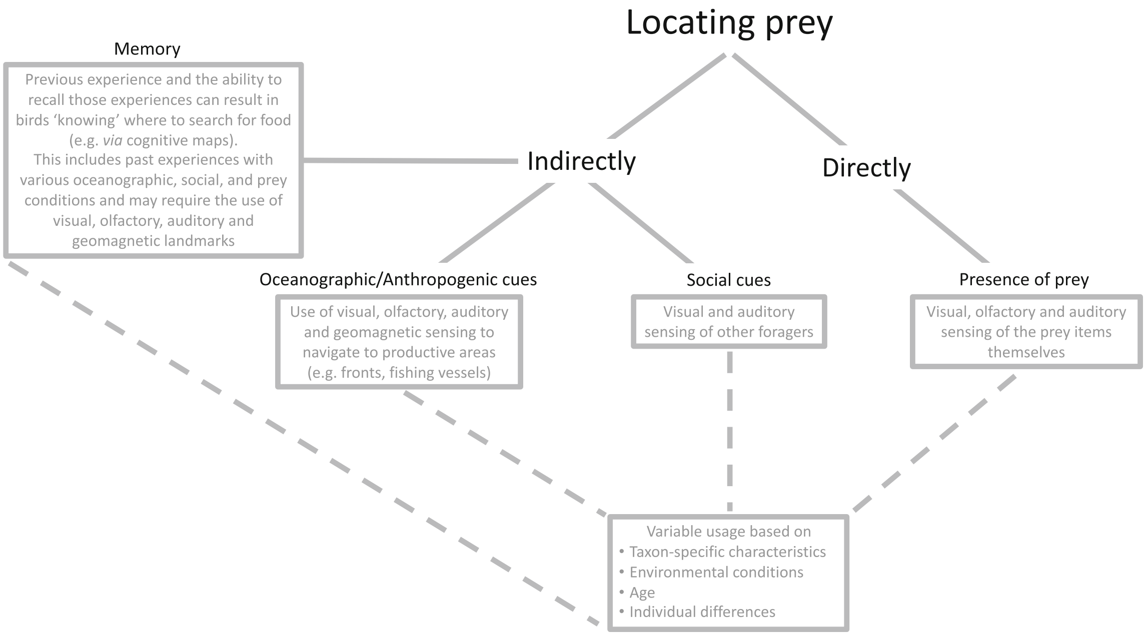

Fig. 1. Birds can search for prey directly using visual, olfactory, and auditory cues. However, seabirds can also look for indicators of the presence of prey. Indirect cues to prey include the use of oceanographic and social cues. The search strategy used may depend on environmental factors such as prey availability, as well as the memory, condition and preferences of the individual bird.

seabirds are gregarious species that breed colonially, form long-term associations (often mating with the same partner year after year), and have been shown to learn from one another. This review does not attempt to define where seabirds fall along the sociality continuum, but rather focuses on one aspect of seabird sociality: the use of social information to find food. In particular, this paper focuses on aggregations of foragers at their nesting colonies and at sea. Herein, these aggregations are considered part of seabird social life because they provide a space where competitive, neutral, and beneficial interactions occur, and are extremely prevalent.

Seabirds are rarely mentioned in the cognition literature, with most avian literature instead focused on corvids, parrots, and species easy to keep in captivity, such as pigeons and chickens. Lambert *et al.* (2022) searched for papers published within a recent five-year window in bird and cognition journals for experiments on any bird species and their 'cognition or relevant psychological phenomenon' (p. 138). Their final list of 567 papers included only 10 seabird species (representing <3% of seabird species), with several seabird orders not represented at all. Additionally, a review of the string-pull task (a commonly used cognitive puzzle where animals must pull a string to obtain a food reward) by Jacobs & Osvath (2015) found only a single account of a seabird, the glaucous-winged gull (*Larus glaucescens*), out of the more than 90 bird species now known to have been tested [ring-billed gulls, *Larus delawarensis*, have since also been tested (Lamarre & Wilson, 2021; Lamarre *et al.*, 2022)].

Given this, it is no surprise that comprehensive reviews of seabird cognitive behaviours are lacking. However, while historically the field of animal cognition has been dominated by experiments, seabird ecology has focused on field observations. This review is not limited to experimental papers (or to specific journals or dates). Instead, this review draws from experiments, theory, and extensive observations of wild individuals from the seabird ecology literature in order to elucidate what is known of seabird cognitive capabilities and the role they play in foraging success.

The present literature review was primarily limited to papers found in *Google Scholar* searches. Example search terms include 'avian', 'bird', or 'seabird' in combination with a common animal cognition term such as 'cognition', 'cooperation', 'coordination', 'intelligence', 'memory', 'neophobia' or 'social'. Relevant studies found within the reference lists of these papers were also included. While beyond the scope of this review, there are additional interesting examples of cognition and discriminatory sensory capabilities in seabirds that are not linked to feeding. These include: tool use for self-care [see Fayet, Hansen & Biro (2020) and the response to Farrar (2020)]; individual recognition (Nevitt, 2008; Curé, Aubin & Mathevon, 2011); and learning/information exchange pertaining to migration, predator prevalence, habitat, and mate choice (Leclaire *et al.*, 2017; Wails & Major, 2017), amongst others. The present review considers studies pertinent only to foraging and foraging cognition.

III. SOCIAL INFORMATION USE

Many seabirds rely on prey that are highly mobile and can be ephemeral: accessible prey swarms may last minutes, hours,

Table 1. Social and other cognitive behaviours that seabirds may use to obtain food. Taken together, these behaviours are representative of a seabird's foraging cognition repertoire. [Correction added on 08 August 2024, after first online publication: Table 1 headers have been amended.]

Social skills and behaviours		
Coloniality	The vast majority of seabirds nest in colonies, interacting with potentially thousands of others daily, and also across years. Information transfer between colony members can influence where individuals feed.	Wakefield *et al.* (2013); Thiebault *et al.* (2014*a*); Sutton *et al.* (2017); Jones *et al.* (2018)
Conspecific and heterospecific attraction	Seabirds use others as cues to food and readily join feeding aggregations (e.g. local enhancement). The presence of others reduces latency to feed and neophobia.	Andersson *et al.* (1981); Hoffman *et al.* (1981); Bairos-Novak *et al.* (2015); Veit & Harrison (2017); García *et al.* (2019); McInnes & Pistorius (2019)
Coordination	Birds have been observed maintaining set inter-individual distances while foraging. Penguins perform synchronous dives and coordinate their movements to corral prey to the surface.	Siegfried *et al.* (1975); Tremblay & Cherel (1999); Ryan *et al.* (2012); Berlincourt & Arnould (2014); Assali *et al.* (2020); Hinke *et al.* (2021)
Responding to/ interpreting another's behaviours and signals	Parents coordinate their individual foraging trips so that there is always one parent at the nest ('turn-taking'). Seabirds are capable of monitoring their partner's behaviour and 'negotiating' the duration of who stays at the nest and who leaves to forage.	Takahashi *et al.* (2017); Storey *et al.* (2020); Gillies *et al.* (2021); McCully *et al.* (2022)
	Pre-dive behaviours may help birds synchronise their dives (e.g. head-dipping in penguins and vocalising in gannets) or avoid collision (vocalising in gannets).	Siegfried *et al.* (1975); Thiebault *et al.* (2019*b*)
	African penguins are capable of following the gaze of conspecifics. This has the potential to help individuals cue into a food item, or coordinate their foraging behaviours. Feeding behaviour in herring gulls is influenced by human behavioural cues, such as gaze direction and the handling of food items.	Nawroth *et al.* (2017); Goumas *et al.* (2019, 2020)
	When leaving the colony to forage, birds may alter their course to follow other foragers or to head in the direction from which a returning forager came. It has been hypothesised that birds can distinguish individuals that have found food from those that have not, based on their circling and diving patterns.	Hoffman *et al.* (1981); Burger (1997); Weimerskirch *et al.* (2010); Thiebault *et al.* (2014*a*)
Non-random social networks	Seabirds form preferences for who to associate with at the species and foraging guild level.	Anguita & Simeone (2016)
Learning		
Refinement of foraging skills	Individual learning: young seabirds learn through the process of exploration. Oblique transmission: young seabirds take foraging cues from (experienced) adults. Cultural transmission: breeding-site-specific foraging behaviours can persist through time, arising from the transfer of information between individuals.	MacLean (1986); Grémillet *et al.* (2004); Riotte-lambert & Weimerskirch (2013); Yoda *et al.* (2011); Wakefield *et al.* (2013, 2019); Mendez *et al.* (2017); Votier *et al.* (2017); Grecian *et al.* (2018); Collet *et al.* (2020); Fayet (2020)
Problem-solving skills		
Problem-solving	Ring-billed gulls are capable of solving string-pull tasks.	Lamarre & Wilson (2021); Lamarre *et al.* (2022)
Tool use	Wild and captive seabirds have been observed bait fishing (placing floating objects on the water to obtain prey).	Ruxton & Hansell (2011)
Plasticity		
Individual differences	Individual differences in the extent social cues are used suggest there are not always fixed behavioural rules.	Berlincourt & Arnould (2014); Thiebault *et al.* (2014*a*); Goumas *et al.* (2019)

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Table 1. *(Cont.)*

Plasticity		
Context-dependent foraging	Seabirds may locate a patch by memory or use a combination of oceanographic, visual, olfactory, and auditory cues to prey (this includes the use of social cues, which can be visual, auditory, or olfactory). The search strategy deployed is often scale dependent: the location of productive areas is often predictable at large and meso scales and so can be learned and memorised, however, after arriving at a productive area seabirds adjust their search behaviour to locate individual patches, utilising strategies such as area-restricted search and social cues. The search strategy deployed can be dependent on environmental conditions and the availability of resources. Seabirds may use different foraging strategies when gathering food for themselves *versus* provisioning their chicks.	Davoren & Burger (1999); Weimerskirch (2007); Montevecchi *et al.* (2009); Regular *et al.* (2013); Bairos-Novak *et al.* (2015)
	'Turn-taking' (see above). The condition of the brooding parent can influence the other parent's foraging bout length and the timing of nest relief.	Takahashi *et al.* (2017); Gillies *et al.* (2021); McCully *et al.* (2022)
Context-dependent associations	The extent to which seabirds utilise local enhancement can be dependent on prey conditions. When the probability of species repeatedly encountering each other is high (e.g. during winter when the community is mainly residents), seabirds have been observed to form preferences for who to feed with at the species level. These preferences relax, however, during migration when the community fluctuates with the comings and goings of migrants (and therefore who a bird will encounter at sea becomes less predictable).	Anguita & Simeone (2015, 2016); Bairos-Novak *et al.* (2015)
Spatial memory		
Cognitive maps	Seabirds can use learned olfactory cues to form 'maps' of the area for navigation.	Reynolds *et al.* (2015)
'Commuting routes'	Seabirds have been observed using repeated flight paths to a patch, suggesting they may 'know' where they are going.	Davoren *et al.* (2003); Weimerskirch (2007); Regular *et al.* (2013); Goyert (2015)

or days (Hoffman *et al.*, 1981; Mackas, Denman & Abbott, 1985; Veit, Silverman & Everson, 1993; Santora, Dorman & Sydeman, 2017). These features make it difficult for birds to locate patches solely using memory and oceanographic features, especially given that the exact location of fronts and other oceanographic features can change (e.g. Ashmole, 1971; Castelao *et al.*, 2006; Billany *et al.*, 2010; Force *et al.*, 2015; Rudeva & Simmonds, 2015; Perelman *et al.*, 2023). It is possible that the location of a food patch can change even in the time it takes a bird to return to its colony and provision its chicks, leaving the bird without knowledge of the patch's new location (Burger, 1997; Weimerskirch *et al.*, 2010). Therefore, social cues could provide seabirds with updated information about the location of prey swarms.

(1) Information transfer at or near colonies

Colony-specific feeding areas are likely maintained by information transfer between colony members, which can result in cultural differences between colonies (Grémillet *et al.*, 2004; Wakefield *et al.*, 2013). Enhanced foraging opportunities *via* social information use may even have led to the evolution of colonial living, or, colonial living may represent a pre-adaptation that allowed terrestrial species to move into marine environments (solitarily defending feeding or breeding territories may be difficult and costly in marine environments where prey can be unpredictable) (reviewed by Evans, Votier & Dall, 2016).

Learning the location of a prey patch while still at (or near) the colony could help a bird find food by reducing the chance that it will head out to search in a suboptimal direction (Burger, 1997; Thiebault *et al.*, 2014*a*; Boyd *et al.*, 2016; Bastos *et al.*, 2020). The number of 'information producers' *versus* 'information scroungers' present likely depends on the advantage to be gained from using social information (Evans *et al.*, 2016), which is likely to change depending on time of year, prey availability, and the condition and characteristics of individual birds (Goodale *et al.*, 2010; Bairos-Novak, Crook & Davoren, 2015; Goyert, 2015; Wakefield *et al.*, 2019). Evans *et al.* (2016) discuss various hypotheses for how information may be transferred at or near a seabird colony. Importantly, however, whether or not an individual intends to share information, it may not be possible to conceal information regarding feeding locations and therefore it can be difficult to rule out information parasitism as a mechanism (Evans *et al*., 2016). Patch location (assessed by the direction in which a bird is coming/going), feeding attempts (e.g. dives), and feeding success (fish in mouth or distended belly) is public information.

Thiebault *et al*. (2014*a*) found that Cape gannets (*Morus capensis*) changed direction in response to conspecifics, either following conspecifics out of the colony or flying in the direction from which they came. Gannets that responded to conspecifics in this way reached their first patch in half the time of those that did not. Sometimes, however, access to such public information may be limited at the colony itself; high noise-to-information ratios can be generated by large numbers of birds arriving at/leaving the colony, or, the comings and goings of others can be obscured by colony ledges (Burger, 1997). Sometimes, the best vantage point for gleaning social information is not at the colony itself, but in the waters immediately surrounding the colony (e.g. Figure 2). Many seabirds leaving the colony stop and 'raft' with other birds, floating nearby before departing to forage. Weimerskirch *et al*. (2010) describe this behaviour in Guanay cormorants (*Leucocarbo bougainvilliorum*) where, remarkably, every one of the study's tracked birds rafted before departing to forage. There was only a single raft of birds present at a given time, and its position changed continuously, orienting towards returning conspecifics. The authors called this a 'compass raft', as it appeared to signal the direction of food patches. It is important to note that not all seabirds make use of social information in this way: Weimerskirch *et al*. (2010) also reported that Peruvian boobies (*Sula variegata*) sharing the same colony as the cormorants (Fig. 2) did not utilise the cormorant raft, or form rafts of their own. However, they likely do make use of other forms of social information, such as local enhancement, as described in Section III.2.

Studies of common (*Uria aalge*) and thick-billed (*Uria lomvia*) murres showed that individuals that had been at the colony the longest (and therefore were more likely to hold outdated information about patch location) were more likely to land in the waters around the colony where rafts form (an area referred to as an 'information halo') than depart to forage directly (Burger, 1997; Elliott *et al*., 2009). A potential confounding observation, however, is that the longer a bird is at a colony, the more soiled its plumage becomes, and soiled individuals may raft to wash (Elliott *et al*., 2009); Thiebault *et al*. (2014*a*) found that all stops on the water by Cape gannets involved comfort behaviours. However, it has been noted that gaining social information and washing are not mutually exclusive, and rafts may serve different purposes for different birds depending on their needs (Burger, 1997; Elliott *et al*., 2009; Weimerskirch *et al*., 2010). The birds utilising the compass raft in Weimerskirch *et al*. (2010) rafted for periods of only a few seconds, so it was suggested that washing was not their goal.

Recent studies have investigated the key question of whether social information shared at and near colonies actually influences where individuals feed. By putting trackers on individual birds, multiple studies have found that individuals leaving the colony together do tend to forage near each other at sea (Cook *et al*., 2017; Sutton *et al*., 2017; Jones *et al*., 2018; Hinke *et al*., 2021).

(2) Locating a patch at sea *via* local enhancement

Even when seabirds do not follow conspecifics from their colony to a patch, they may still exhibit conspecific attraction (e.g. choosing populated food piles over food piles with no other birds present; Andersson, Gotmark & Wiklund, 1981) and associate with others at sea (Tremblay & Cherel, 1999; Davoren, Montevecchi & Anderson, 2003; Berlincourt & Arnould, 2014). Feeding birds can be incredibly conspicuous: aggregations of seabirds around prey swarms may involve thousands, sometimes over one million, individual birds (Hoffman *et al*., 1981; Veit & Hunt Jr, 1991; Camphuysen & Webb, 1999; Camphuysen, Scott & Wanless, 2006) that knowingly or unknowingly transmit information about where, what, and how to forage (Galef & Giraldeau, 2001). In this way, information can be transferred at sea between individuals that do not share a colony.

When the presence of a forager draws the attention of other foragers to a patch, this is known as local enhancement (Veit & Harrison, 2017). It is evident that at-sea feeding flocks are largely the result of birds cueing into the presence of others, and not merely a product of birds discovering patches individually (Fig. 3) (Hoffman *et al*., 1981; Camphuysen, 2011; Thiebault *et al*., 2014*a*; McInnes & Pistorius, 2019). Thiebault *et al*. (2014*b*) observed that large aggregations of predators could increase patch-detection distances by 1650% compared to solitary detection of a patch. An experiment by Bairos-Novak *et al*. (2015) quantified the use of local enhancement and found that the presence of decoys on the water was up to 17 times more likely to elicit a response from birds (circling, landing, etc.) relative to controls. Similar results have been obtained from observational studies: McInnes & Pistorius (2019) found a strong relationship between penguins and flying birds at sea (flying birds arrived quicker in response to larger groups of diving penguins) independent of prey biomass. Some research suggests that seabirds generally do not search for prey directly, but instead look for indicators of the presence of prey, likely forming search images of other predators (Haney, Fristrup & Lee, 1992; Tremblay *et al*., 2014); using a combination of GPS (global positioning system) and camera data, Tremblay *et al*. (2014) found that >90% of birds in their study were associated with other predators (the main drivers of the movements of Cape gannets were other gannets, dolphins, and fishing boats, with only three birds observed foraging alone). The authors were able to rule out olfaction as a mechanism of patch detection by analysing wind direction.

Haney *et al*. (1992) and Thiebault *et al*. (2014*b*) calculated the theoretical distance at which birds can visually detect

Fig. 2. Nesting colony of Guanay cormorants (*Leucocarbo bougainvilliorum*) (black individuals) and Peruvian boobies (*Sula variegata*) (smaller aggregations of white birds, on the right). Arrow points to the cormorant at-sea compass raft. Image from Weimerskirch *et al.* (2010), used with permission from PLoS under the terms of the Creative Commons License: https://creativecommons.org/licenses/by/4.0/legalcode.

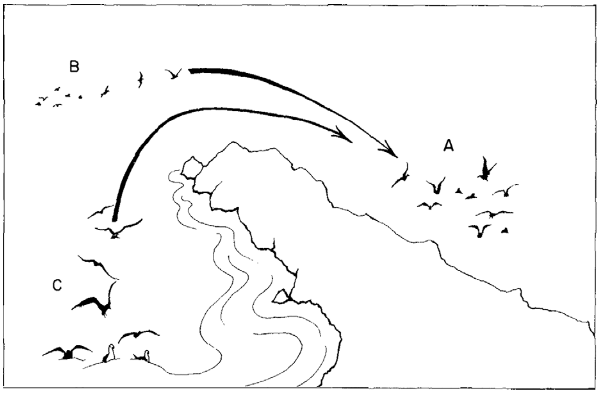

Fig. 3. Seabirds utilise social cues to locate prey swarms. Patch-finding predators catch the attention of other predators, alerting them to the patch, a phenomenon known as local enhancement; the approaching birds benefit from the conspicuousness of the others. In this image, Group A draws in Group B. Group C cannot see Group A or the patch itself, but takes cues from Group B, demonstrating the utility of at-sea associations in locating even distant patches. Image from Hoffman *et al.* (1981), licensed under STM guidelines by permission of Oxford University Press.

conspecifics at sea to be between ~1 and ~49 km depending on the activity of both the observer and observee. These same studies also empirically measured recruitment of individual birds to flocks at sea: Thiebault *et al.* (2014*b*) observed flying Cape gannets responding to large flocks (100–150 gannets) from ~38 km away (while distances were much shorter for the detection of smaller groups of sitting birds). In general, however, observed recruitment distances tended to be lower than the theoretical maximum. However, as noted by these authors, data from the field reflect when a bird decides to begin moving towards a flock, not necessarily when that bird first detects the flock (which could happen from further away), therefore, observed reaction distances may be closer to minima. Wandering albatrosses (*Diomedea exulans*) have also been found to be attracted to (i.e. fly towards) fishing vessels nearly 30 km away, beyond which distance trajectories were random with respect to the ship's location (Collet, Patrick & Weimerskirch, 2015).

Importantly, feeding frenzies can be noisy, and so local enhancement need not be strictly visual (Putland, Atkins & Radford, 2016; Choi *et al.*, 2017; Thiebault *et al.*, 2019*a*,*b*). Putland *et al.* (2016) detected nine different feeding flock sounds, including 'thumps' and 'high frequency squeals' from gannets, 'buzzes', 'moans' and 'whistles' from cetaceans, and 'grunts' and 'pops' from fish. These sounds were determined to be within the hearing range of many marine predators and thus may serve as cues to the existence/location of prey swarms. Subsurface predators can cue into underwater sounds produced by swimming and diving species, while volant birds can make use of sounds produced by surfacing mammals as well as other birds vocalising on the water and in the air above prey schools. Anthropogenic noise pollution can mask such acoustic cues, however, and negatively affect where and when these predators feed (Clark *et al.*, 2009; Pichegru *et al.*, 2017; Anderson Hansen *et al.*, 2020; Sørensen *et al.*, 2020; Duarte *et al.*, 2021).

(3) Coordination

Local enhancement is generally opportunistic (birds move towards others when they see them) and information is transferred passively (feeding flocks are public information); in seabirds, coordinated/cooperative foraging appears to be rarer. At its simplest, coordinated behaviour need not arise from complex mechanisms. Models have shown that group behaviour, such as flocking and pack hunting, can be generated from relatively simple behavioural rules that do not require a complex social structure or communication between individuals [i.e. by simply sensing one another, with individuals acting independently (e.g. Hamilton, 1971; Muro *et al.*, 2011)]. The extent to which coordination amongst seabirds rises beyond such simple rules is not well understood, although some authors have suggested that seabirds coordinate while foraging in ways that are sustained and non-random.

Spatial analyses of radar images show that birds maintain set inter-individual distances to scan efficiently for prey, which requires they coordinate their flight speed and bearings. These flights have consistent temporal and spatial attributes that 'cannot occur by chance' (Assali, Bez & Tremblay, 2020, p. 1). Regardless of how such coordination is achieved, however, an individual's position within such a group can still be non-random. Wakefield *et al.* (2019), for example, found that adult gannets tended to lead foraging flocks more often than immatures and suggested that immatures follow in order to gather information, after ruling out biomechanical benefits as an explanation.

Primarily, coordination and cooperation has been suggested in penguins that herd fish (Fig. 4) and perform synchronous dives (Fig. 5) (Siegfried *et al.*, 1975; Tremblay & Cherel, 1999; Pütz & Cherel, 2005; Ryan, Edwards & Pichegru, 2012; Berlincourt & Arnould, 2014; McInnes *et al.*, 2017; Hinke *et al.*, 2021). The lasting duration of these synchronizations suggests they may be governed by more than simple rules: Hinke *et al.* (2021) observed synchronised dives in at least two chinstrap penguins (*Pygoscelis antarcticus*) for more than 9 h in a single foraging bout (see Fig. 5). Their synchronicity decreased at night, presumably because of the difficulty of maintaining visual contact in the dark. Tremblay & Cherel (1999) similarly reported two northern rockhopper penguins (*Eudyptes moseleyi*) performing an incredible 286 synchronous dives during a 7-h period (representing >90% of their total dives during this period). In other penguin species, head-dipping behaviour has been observed as birds prepare to dive, which may serve as a cue to synchronise diving (e.g. African penguins, *Spheniscus demersus*, in Siegfried *et al.*, 1975). Given the small number of individuals these studies tracked, it has been argued that the probability of observing such synchronised behaviours would be low if they were not common occurrences; existing data thus likely underestimates the prevalence of group foraging (Pütz & Cherel, 2005; Sutton *et al.*, 2017; Assali *et al.*, 2020).

Importantly, it should be noted that coordination does not necessarily involve cooperation. If birds that coordinate their movements obtain more food, they may continue to do so for entirely selfish reasons (i.e. they may not assist or share with others). While the evidence for cooperative/coordinated hunting in seabirds is compelling, it is based primarily on observational evidence. Future work should explicitly test the limits of seabirds' capacity for cooperation experimentally by breaking this complex behaviour down into its simpler components [as has been done in other aquatic and semi-aquatic species (Ladds, Hoppitt & Boogert, 2017; Schmelz *et al.*, 2017; King *et al.*, 2021)]. For example, an experiment by Nawroth, Trincas & Favaro (2017) showed that captive African penguins are capable of following the gaze of conspecifics. While the ability to follow another's gaze alone is not evidence that this species engages in cooperation, gaze following is a potentially relevant building block of cooperation. Nawroth *et al.* (2017) argue for similar experiments to be conducted in other seabird species that have a variety of social structures to improve our understanding of the adaptive significance of such behaviour. Future work should continue to evaluate seabird social behaviours under controlled experimental conditions to help place existing observations of coordinated foraging into context, and to clarify what seabirds are cognitively capable of *versus* the manifestation of those abilities in the real world.

Another example of cooperation and coordination is biparental care in the form of 'turn-taking'. In many seabird species, one parent stays at the nest while the other is out foraging, and, after the forager returns, the roles reverse. Partners do not always follow a predictable schedule, suggesting that the timing of this switch is not fixed. Recent work shows that seabirds can actively monitor their partner's behaviour, coordinating and negotiating the duration of who stays at the nest and who goes out to sea (Takahashi *et al.*, 2017; Johnstone & Savage, 2019; Storey, Wilhelm & Walsh, 2020; Gillies *et al.*, 2021; McCully *et al.*, 2022).

A forager may be responding its own hunger levels when setting its foraging trip length, however, if there was no coordination between parents we might expect this (or some other internal/environmental cue) to be the only factor determining trip lengths, and this is not the case. Several studies have concluded that a forager's trip length is influenced by the condition of the brooding parent back at the nest (Gillies *et al.*, 2021; McCully *et al.*, 2022) and that the brooder may be actively communicating its body condition to the forager (Takahashi *et al.*, 2017).

The brooding partner can either abandon the nest to forage after a fixed amount of time, wait potentially indefinitely for the foraging partner to return, or wait until its own hunger/body condition declines to some threshold level. Any of these could represent a fixed response by the brooder but brooders do not predictably follow any one of these options all of the time [i.e. nest relief interactions can be 'irregular' (Storey *et al.*, 2020) and turn-taking is 'imperfect' (Johnstone & Savage, 2019)] suggesting that these birds are not constrained to follow a strict behavioural rule. Coordination strength ('how closely trip durations or nest attendance patterns are matched within pairs'; McCully *et al.*, 2022, p. 2) varies both within and across seabird species. The ability of parents to cooperate in this way and coordinate

Fig. 4. African penguins (*Spheniscus demersus*) feeding in a clockwise pattern that suggests coordination. At the centre of these aggregations, fish were sometimes visibly corralled to the surface. Other seabird species have joined the swimming penguins, aerially exploiting the newly surfaced fish. Image from Ryan *et al.* (2012), used with permission from Ardea (Netherlands Ornithologists' Union).

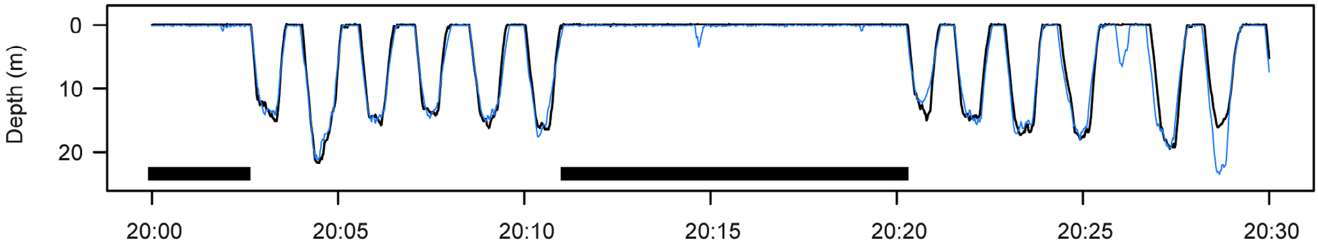

Fig. 5. Example of synchronised dives performed by two chinstrap penguins (*Pygoscelis antarcticus*). Time is on the *x*-axis, the male line (blue) extensively overlaps with the female line (black), black bars along the *x*-axis indicate surfacing. Video footage revealed a third individual was also often present. Figure from Hinke *et al.* (2021), used with permission under the terms of the Creative Commons license: https://s100.copyright.com/AppDispatchServlet?title=Serendipitous%20observations%20from%20animal-borne%20video%20loggers%20reveal%20synchronous%20diving%20and%20equivalent%20simultaneous%20prey%20capture%20rates%20in%20chinstrap%20penguins&author=Jefferson%20T.%20Hinke%20et%20al&contentID=10.1007%2Fs00227-021-03937-5&copyright=This%20is%20a%20U.S.%20government%20work%20and%20not%20under%20copyright%20protection%20in%20the%20U.S.%3B%20foreign%20copyright%20protection%20may%20apply&publication=0025-3162&publicationDate=2021-07-24&publisherName=SpringerNature&orderBeanReset=true&oa=CC%20BY.

their foraging efforts is likely to have a significant impact on individual fitness, because it will directly affect the number of chicks fledged (Morris, 1987), with a failure to coordinate leading to starvation or predation of the chicks.

IV. VARIATION IN SOCIAL INFORMATION USE

There is variation in a seabird's propensity to forage in flocks *versus* locating prey *via* another, non-social, foraging strategy. However, the vast majority of seabird species readily join aggregations and use local enhancement, with existing variation being more in the way and extent to which this behaviour occurs rather than whether it occurs at all.

Why such variation exists is of interest. Birds may locate a patch simply because they follow other birds indiscriminately, however, a more reliable cue to prey would be to learn to follow particular species or individuals performing specific behaviours. If seabirds are not associating with all species or individuals equally or randomly, this might imply the existence of mechanisms more complex than fixed, simple conspecific attraction.

(1) Non-social foraging tactics

While the use of social cues is increasingly being recognised as an important strategy by which seabirds find food, a variety of search strategies have been documented (Fig. 1). Direct cues include locating prey by smell (Hutchison & Wenzel, 1980; for review see Nevitt, Losekoot & Weimerskirch, 2008) and/or sight (e.g. *via* area-restricted search; Weimerskirch *et al*., 2007). One important odorant is dimethyl sulphide, which can serve as an indicator of plankton (Owen *et al*., 2021). Many seabirds, notably Procellariiformes (Nevitt, Veit & Kareiva, 1995) and penguins (Culik, 2001; Wright, Pichegru & Ryan, 2011), are attracted to this scent although individual species, even within Procellariiformes, vary in the extent of this attraction (Nevitt *et al*., 1995). Birds that use their sense of smell to detect their prey should approach from downwind, and therefore can be distinguished from those relying on visual cues which should approach from random directions with a line of sight (as in Nevitt *et al*., 1995, 2008; Thiebault *et al*., 2014*b*). In experiments in which a bird's sense of smell was temporarily disabled to test their reliance on olfaction, Padget *et al*. (2017) showed that wild Scopoli's shearwaters (*Calonectris diomedia*) were able to forage successfully despite losing the ability to smell. Nocturnal and crepuscular birds have larger olfactory bulbs than diurnal birds (Healy & Guilford, 1990), suggesting that olfaction might be particularly important for nighttime foragers less able to rely on visual cues. Conversely, daytime forgers (with less well developed nostrils than 'tube-nosed' Procellariiformes), likely rely more heavily on visual cues (e.g. gannets; Thiebault *et al*., 2014*b*). However, the fact that even visually hunting species such as gannets do not always associate themselves with the clearest waters (where prey are most visible) suggests they use additional cues to find prey (Tremblay *et al*., 2014).

Seabirds can use memory of prior experiences as well as oceanographic cues to locate a prey patch (Davoren *et al*., 2003; Force *et al*., 2015; Wakefield *et al*., 2015). Evidence for this includes the use of 'commuting routes' (i.e. regular flight paths), which suggest the birds 'know' where they are going (Irons, 1998; Davoren *et al*., 2003; Weimerskirch, 2007; Regular *et al*., 2013; Goyert, 2015). Such strategies may be particularly useful when prey are benthic and relatively stationary (e.g. Cook, Cherel & Tremblay, 2006). Seabirds likely use memory and oceanographic cues to locate broad areas that are predictably high in resources, within which the presence and behaviours of other foragers provide indirect cues to specific prey patches (Davoren *et al*., 2003; Thiebault *et al*., 2014*a*; Wakefield *et al*., 2015; Anguita & Simeone, 2016).

Several modelling studies have shown that birds perform 'optimally' when a mixture of search strategies is used (Boyd *et al*., 2016; Bastos *et al*., 2020). Whichever search strategy is used principally concentrates the predators (e.g. birds converging on an odour) and thus facilitates local enhancement because larger densities of birds are more conspicuous (Thiebault *et al*., 2014*b*; Boyd *et al*., 2016; Bastos *et al*., 2020). Whether a bird prioritises one sense over another is not fixed and birds can use their senses in different ways (e.g. visually searching for prey directly or visually searching for other foragers).

(2) Social information use across species

The extent to which seabirds forage socially *versus* solitarily varies considerably across species (Hoffman *et al*., 1981; Porter & Sealy, 1981; Briggs *et al*., 1987; Ainley & Boekelheide, 1990; Harrison *et al*., 1991; Camphuysen & Webb, 1999; Silverman & Veit, 2001; Camphuysen *et al*., 2006; Bairos-Novak *et al*., 2015). For example, in the sub-Antarctic, Silverman & Veit (2001) found that while diving-petrels made up ~33% of the birds surveyed, they comprised <2% of bird aggregations. By contrast, black-browed albatrosses (*Thalassarche melanophris*) participated in flocks disproportionately given their abundance (Harrison *et al*., 1991; Silverman & Veit, 2001; Silverman *et al*., 2004). Seabirds also differ in their propensity to join flocks of their own species *versus* mixed-species flocks (Briggs *et al*., 1987). This has been demonstrated experimentally by Bairos-Novak *et al*. (2015) who found that not all species used local enhancement equally: the presence of decoys was ~four times more likely to elicit a response in common murres, ~seven times more likely in Atlantic puffins (*Fratercula arctica*), and ~seventeen times more likely in northern gannets (*Morus bassanus*). The magnitude of the responses also varied depending on whether or not the species of decoy matched the species of bird.

Camphuysen & Webb (1999) and Camphuysen *et al*. (2006) described the propensity of various species to join feeding flocks and offered possible explanations for the observed variation: small species such as storm-petrels and terns may avoid joining (or only join at the periphery) in the presence of larger/more competitive species. Scroungers, however, such as large gulls and skuas, profit by pirating and are more likely to seek flocks out.

Some species may be seen in flocks frequently, not because of their propensity to join, but because of their propensity to initiate, i.e. particular species or individuals may represent a preferred cue because of their patch-finding aptitude. Deep-diving swimming species such as auks (as well as tuna and marine mammals) are sometimes referred to as flock 'producers' as they are often the first to locate a prey swarm and drive it to the surface within reach of flying birds (Fig. 4) (Ashmole, 1971; Hoffman *et al*., 1981; Camphuysen & Webb, 1999; Camphuysen *et al*., 2006; Hebshi, Duffy & Hyrenbach, 2008; Goyert, Manne & Veit, 2014; Veit & Harrison, 2017; McInnes & Pistorius, 2019). McInnes & Pistorius (2019) found a strong relationship between penguins and flying birds, with flying birds arriving more quickly in response to larger groups of diving penguins, and this relationship was independent of prey biomass.

Some species or individuals may serve as good cues because of their conspicuous size or coloration (Bretagnolle, 1993; Beauchamp & Heeb, 2001; Silverman *et al*., 2004; Weimerskirch *et al*., 2010; Bairos-Novak *et al*., 2015). Within

Procellariiformes, Bretagnolle (1993) found that white species had the highest levels of intra- and interspecific associations. Contrasting black-and-white colouring is also conspicuous and has been suggested to help penguins maintain visual contact underwater where light levels are low (Tremblay & Cherel, 1999). Weimerskirch *et al.* (2010) speculated that colour patterning may affect social information use: the dark plumage of Guanay cormorants makes them cryptic at a distance and thus social information may be transferred more effectively at near-colony rafts than at sea. Peruvian boobies, however, are largely white (Fig. 2), so while they do not appear to utilise compass rafts, their conspicuousness may advertise patch location *via* local enhancement. Age-related differences in seabird coloration have also been argued to function as an indicator of social status, with darker juveniles being submissive to their lighter adult counterparts (Bretagnolle, 1993). Under the assumption that juveniles are also less-skilled foragers than adults, selectively following whiter individuals may be a way of filtering out young birds in favour of associating with older, more experienced, individuals. Conspicuous coloration could be selected for as long as the benefits (e.g. finding a patch by cueing into conspecifics, group dynamics that facilitate prey capture, maintaining flock cohesion) outweigh the cost of advertising one's location (see Section V on how competitive interference at a patch can be mitigated); those that can learn to utilise such visual cues should then be favoured.

Flock 'catalysts' are species whose conspicuous presence rapidly leads to flock formation. Black-browed albatrosses (Silverman & Veit, 2001; Silverman *et al.*, 2004) and black-legged kittiwakes (*Rissa tridactyla*) (Hoffman *et al.*, 1981; Camphuysen & Webb, 1999; Camphuysen *et al.*, 2006) have been observed playing such a role. Hoffman *et al.* (1981) suggest that birds can distinguish kittiwakes that have found a patch from those that have not, based off their dive patterns: a single dive by a kittiwake could suggest that no prey was present or that only a single prey item was found, while circling back may indicate the kittiwake had found a school of fish; when a kittiwake dived but did not circle back other birds tended not to respond to its behaviour. This raises the idea that local enhancement may be more nuanced than its usual textbook description as simple conspecific attraction, and could involve more complex forms of social learning such as interpreting another's behaviour. For example, birds may find a patch simply because they follow other birds indiscriminately, however, a more reliable cue to the presence of prey would be to follow specific species performing specific behaviours, such as a kittiwake diving then circling back to dive again. Furthermore, associations between particular species have been shown to be stable through time (Anguita & Simeone, 2016) suggesting that seabird associations are not always random but instead they can form preferences. The extent to which seabirds rely upon specific cues (positive associations that they are predisposed to respond to or that result from coevolution) *versus* generalise across cues (a more cognitively complex process), is still not well understood.

(3) Social information use within species (age effects and individual differences)

The use of social learning can vary among individuals, and with the life stage of the demonstrator and observer (Greggor, Thornton & Clayton, 2017). Once a bird reaches breeding age, it is generally not possible to age the bird visually without using ringing or other marking techniques. However, technological advancements in solar-powered trackers with remotely downloadable data have made it possible to track individuals at sea over extended periods, as the bird does not have to be re-captured to retrieve the data. It is therefore now possible to track how feeding behaviour changes as a function of age/experience.

Knowledge of the extent to which juveniles and adults practice local enhancement may provide clues as to how this behaviour is acquired. If there is a learned component to this behaviour, rather than an evolutionary predisposition to attend to certain cues or an environmental trigger, we may expect an increased reliance on local enhancement with age or experience or that different age classes attend to different cues. For example, adults may be able to use more subtle or complex cues, enabling them to find less-obvious patches. Different foraging behaviours have indeed been observed across age classes (Weimerskirch *et al.*, 2014; Mendez, Prudor & Weimerskirch, 2017; Votier *et al.*, 2017; Grecian *et al.*, 2018; García *et al.*, 2019) and positive relationships between foraging efficiency and age documented (MacLean, 1986; Berón *et al.*, 2013; Péron & Grémillet, 2013; Riotte-lambert & Weimerskirch, 2013; Fayet *et al.*, 2015). While the development of socio-cognitive skills has been suggested as a mechanism (Yoda *et al.*, 2011; Mendez *et al.*, 2017; Wakefield *et al.*, 2019), direct evidence would likely require (*i*) experiments showing that specific socio-cognitive skills (e.g. the ability to learn by observing others, or the ability to recognise/remember individuals) improve as a function of age or experience, and (*ii*) a positive relationship between an individual's performance on these cognitive tests and foraging success.

Wakefield *et al.* (2019) found that immature gannets travel in flocks more often than adults but also that flocks are disproportionately led by adults, presumably because younger birds are less experienced and knowledgeable. If there is a critical learning period where young birds learn the various nuances of foraging and local enhancement (akin to songbirds developing their vocal repertoires) future studies might investigate whether early life adversity (e.g. a bad krill year during this learning period) affects foraging skills later in life [see Fay *et al.* (2015) for an example of how early-life adversity can affect survival differentially based on sex and age]. It is, however, likely that a seabird's extended juvenile period of several years (Weimerskirch *et al.*, 1987; Fay *et al.*, 2016) allows them to learn how to forage in both good and bad years, so they enter adulthood with a more complete foraging skill set.

As noted by Tremblay *et al.* (2014), juvenile seabirds likely play an important role in the at-sea predator community:

while breeding birds must leave a patch to return to the colony, non-breeders are a more permanent presence at sea. Because these individuals can remain at patches for longer than their breeding counterparts, and because the number of birds at a patch increases patch conspicuousness, non-breeders may play a key role in facilitating local enhancement. More research is needed on the utility of juveniles as a cue to the presence of prey: while the presence of any foraging individuals can be a cue to prey, actively foraging adults may be a preferred cue. Indeed, as juveniles explore and refine their skillsets, they may not even utilise the same foraging grounds as adults (Péron & Grémillet, 2013; Riotte-lambert & Weimerskirch, 2013; Weimerskirch *et al.*, 2014; Fayet *et al.*, 2015; Votier *et al.*, 2017; Grecian *et al.*, 2018).

Understanding individual variation in behaviour is important (Thornton & Lukas, 2012), but studies on the extent to which seabirds forage socially *versus* solitarily have historically been lacking because of the difficulty associated with recognising and tracking individuals at sea. Miniaturised tracking devices with cameras (e.g. Figure 6) (Yoda *et al.*, 2011; Thiebault *et al.*, 2014*a*; Tremblay *et al.*, 2014; Brisson-Curadeau *et al.*, 2018; Hinke *et al.*, 2021) now make such studies possible. For example, Thiebault *et al.* (2014*a*) documented Cape gannets using social information to update their flight path (either by following an outbound conspecific or flying in the direction of a returning conspecific). Some birds never responded to others in this way, while others did so up to 14 times per hour.

(4) Interactions between social information use and the environment

Seabirds today are affected by a multitude of stressors from changing climate to changing prey availability, and these changes are occurring at alarming rates (Paleczny *et al.*, 2015; Sydeman *et al.*, 2015*b*,*a*; Poloczanska *et al.*, 2016; Grémillet *et al.*, 2018); both predators and prey may be approaching their thermal tolerance limits. The same environmental factors that affect prey availability likely also affect seabird social information use when birds use social cues to find prey. Importantly, there is some evidence that the propensity to feed in flocks may vary with sea surface temperature, with fewer interspecific associations forming in warmer years (Ainley *et al.*, 1990; Monier *et al.*, 2020). This relationship between temperature and seabird feeding flocks warrants more detailed investigation, for both cold and warm water species, while controlling for prey availability over long time frames. Weather conditions such as precipitation or swell height can also affect the ability of birds to see, and therefore utilise, one another while foraging (Haney *et al.*, 1992). This can impact local enhancement usage both at small (*via* localised weather conditions) and large scales (*via* the climatic conditions of a region). Given the importance of these foraging interactions to foraging success, there are potentially serious implications for the conservation of these taxa. Seabird social foraging interactions are likely vulnerable to changing abiotic and biotic environmental conditions.

Two recent modelling studies examined the effectiveness of social information use as a foraging strategy under different prey concentrations. Boyd *et al.* (2016) modelled foraging success and trip duration when birds located a patch by following conspecifics out of the colony, by local enhancement, or by a combination of both. Compared to a model with no social information use, following outbound conspecifics reduced failure rates but only reduced trip duration when prey was spatially concentrated (trip duration was not affected when prey was broadly distributed). Conversely, the local enhancement strategy did not affect failure rate or trip duration when prey was broadly distributed, but improved both when prey were spatially concentrated. Each of these strategies was more effective when bird density was higher. The best strategy in terms of reduced trip failure and duration was when both strategies were used in conjunction: following outbound conspecifics facilitated local enhancement by concentrating the birds in the same general area, often close to the colony. A second modelling study (Bastos *et al.*, 2020) compared the use of olfactory cues to local enhancement and also found that the best search strategy was to use both in conjunction. When foraging conditions were good the two strategies were equally effective, although as in Boyd *et al.* (2016) the utility of local enhancement was dependent on relatively high bird densities. Under poor foraging conditions, individuals were unable to find resources regardless of their search strategy. Under baseline conditions, however, the local enhancement model was more effective than olfaction alone. The results of these modelling studies are supported by an experiment using wild birds by Bairos-Novak *et al.* (2015): common murres were found to use local enhancement less often when prey could be reliably located.

For breeding birds, prey capture requirements change seasonally when there are chicks to provision. This likely affects their foraging strategy and the extent to which they forage socially. In rhinoceros auklets (*Cerorhinca monocerata*), for example, Davoren & Burger (1999) reported mixed-species foraging when gathering food for themselves, but primarily solitary foraging when provisioning their chicks. The authors suggest a trade-off: solitary foraging meant diving deeper for less-obvious prey but led to larger catches and likely reduced the chances of losing a meal to pirates. Juveniles may have less to lose from an unsuccessful foraging trip than breeders with chicks to feed, thus, juveniles and adults may exhibit varying risk-sensitivity and foraging patterns (de Grissac *et al.*, 2017).

Importantly, even if the extent to which an individual utilises social information does not change, who a bird gets its information from can change. For example, when the probability of species repeatedly encountering one another at sea is high (e.g. resident species encountering other resident species), seabirds have been observed to form preferences for who to feed with at the species level. During the migration season, however, when the predator community fluctuates with the comings and goings of migrants and becomes less predictable, seabird associations became more random, with seabirds broadening their preferences

Fig. 6. The deployment of miniaturised tracking devices outfitted with GPS (Global Positioning System) and cameras allows for investigations into individual differences in social information use. Compiled from images from Thiebault *et al.* (2014*a*), licensed under STM guidelines by permission of Oxford University Press.

of who to feed with, although still tending to associate with species of their same size and foraging guild (Anguita & Simeone, 2016).

V. THE BENEFITS OF SOCIAL INFORMATION USE

It may seem counterintuitive that large groups of individuals congregating at a patch can result in foraging gains, however, competition over resources assumes resource limitation. If a patch has a sufficiently high prey density, there may be few to no competitive costs. Seabird food patches can be large enough that they cannot be monopolised and support thousands of predators (Hoffman *et al.*, 1981; Veit & Hunt Jr, 1991; Camphuysen & Webb, 1999; Camphuysen *et al.*, 2006). Thiebault *et al.* (2016, p. 163) stated that 'gannets foraging in a school likely do not compete much for food' given that the number of fish an individual needs is much smaller than the total number of fish in a school. Their calculations for gannets breeding on Bird Island, South Africa, suggest that adults only need to catch ~seven sardines per day to provision themselves and their chick, with non-breeding birds needing even fewer. Furthermore, the negative effects of competition at a patch may be countered or outweighed by the fact that the presence of competitors is what facilitated patch discovery *via* local enhancement.

That seabird social foraging interactions can be beneficial has been demonstrated theoretically (Buckley, 1997; Grünbaum & Veit, 2003; Boyd *et al.*, 2016; Bastos *et al.*, 2020), experimentally (Andersson *et al.*, 1981; Gotmark, Winklet & Malte, 1986; Bairos-Novak *et al.*, 2015; García *et al.*, 2019), and observationally (Hoffman *et al.*, 1981; Harrison *et al.*, 1991; Camphuysen & Webb, 1999; Silverman *et al.*, 2004; Camphuysen *et al.*, 2006; Thiebault *et al.*, 2014*a*, 2016; McInnes *et al.*, 2017; McInnes & Pistorius, 2019); see Veit & Harrison (2017) for a recent review. Even the patch-finder, i.e. the individual with perhaps the most to lose if a patch becomes shared, can benefit from others joining its flock (Evans, 1982; Gotmark *et al.*, 1986).

It has been empirically demonstrated that at-sea interactions provide concrete foraging benefits such as increased patch detection (Thiebault *et al.*, 2014*b*) and decreased search time (Thiebault *et al.*, 2014*a*). Thiebault *et al.* (2014*b*, p. 1308) stated that 'congregating in high densities might be crucial for seabird foraging efficiency' after observing that predators aggregating at a feeding site may increase patch detection distances by 1650% compared to direct detection of prey. Thiebault *et al.* (2014*a*) found that Cape gannets that used social information to update their foraging route reduced the time they spent searching for their first patch by half compared to gannets that did not. Social foraging can also enhance prey capture (Gotmark *et al.*, 1986; Thiebault *et al.*, 2016; McInnes *et al.*, 2017). Gotmark *et al.* (1986) found increased hunting success with flock size of wild-caught black-headed gulls (*Larus ridibundus*), due to the fish becoming more dispersed when hunted by flocks compared to lone gulls. Similarly, Thiebault *et al.* (2016) found that isolated dives of wild gannets were always less successful than dives that occurred in the context of a flock. Accompanying models of fish schools showed that the prey become disorganised after the first attack. Additionally, the presence of others at a feeding site has been shown to reduce neophobia and latency to feed (Andersson *et al.*, 1981; García *et al.*, 2019).

Taken together, these results support the idea that changes to the predator community have the potential to impact foraging success as much as changes in prey availability (Tremblay *et al.*, 2014; Goyert *et al.*, 2018). A role of Allee effects has been suggested (Grünbaum & Veit, 2003; Ryan *et al.*, 2012; McInnes *et al.*, 2017), for example, a feedback loop where declines in bird abundance lead to decreased foraging success, which then feeds back to affect abundances further (Fig. 7). Such density dependency would make local populations particularly vulnerable to extinction. Given that interspecific associations may be as important as intraspecific associations for many foraging seabirds, this is a taxa-wide conservation issue.

Species that participate in large feeding flocks have likely coevolved to do so, with competitive interference at a patch mitigated *via* behavioural modifications and niche segregation (Harrison & Whitehouse, 2011; Bronstein, 2015; Thiebault *et al*., 2016, 2019*b*; Sanchez *et al*., 2018). Furthermore, even if an individual, acting alone, could be considered an exploiter/competitor, collective actions can produce a net benefit and promote coexistence (Palmer *et al*., 2015). For example, groups of deep-diving species such as penguins, tuna, and cetaceans can break up swarms and drive prey to the surface into the reach of species that cannot dive as deep (Ashmole, 1971; Camphuysen *et al*., 2006; Veit & Harrison, 2017). It should also be noted that there may be fewer competitive costs associated with feeding in a mixed-species flock than in a single-species flock because the different species are likely to exhibit slightly different prey-capture strategies and preferences (Ashmole & Ashmole, 1967;

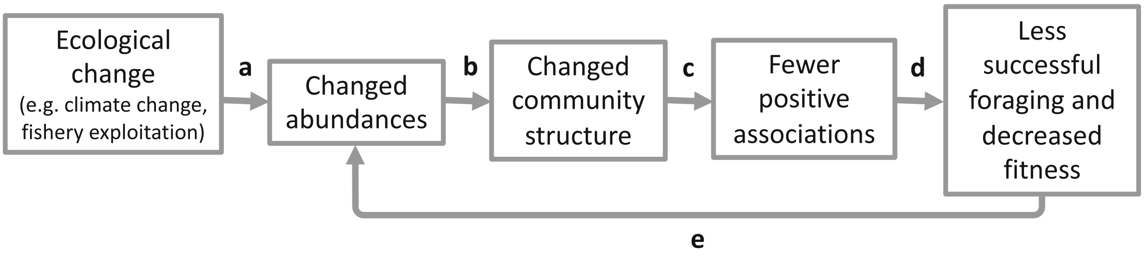

Fig. 7. Proposed feedback loop. Changing species interactions may originally be driven by ecological change altering abundances (links a–c), but the consequences of the changed interactions (link d) may feed back (link e) and drive further changes to abundances, community structure, and species interactions. Image from Monier *et al*. (2020), with slight modifications. Used with permission under the terms of the Creative Commons License: https://s100.copyright.com/AppDispatchServlet?title=Changes%20in%20positive%20associations%20among%20vertebrate%20predators%20at%20South%20Georgia%20during%20winter&author=Samantha%20A.%20Monier%20et%20al&contentID=10.1007%2Fs00300-020-02720-4&copyright=The%20Author%28s%29&publication=0722-4060&publicationDate=2020-07-23&publisherName=SpringerNature&orderBeanReset=true&oa=CC%20BY.

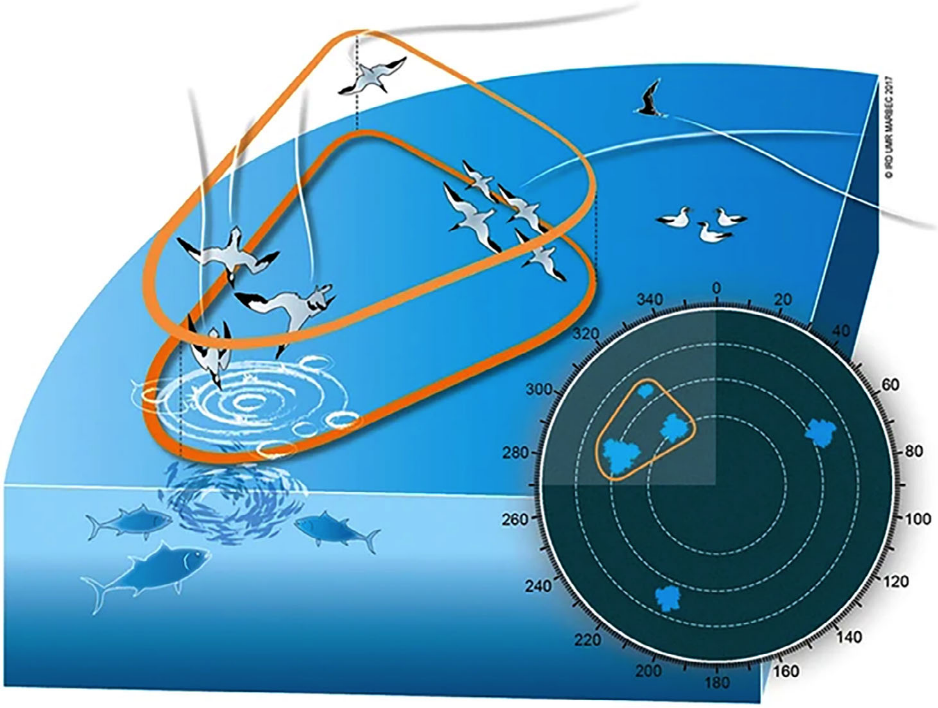

Fig. 8. An illustrative example of foraging seabirds and an associated image from a ship's radar, showing seabird echos. Image from Assali *et al*. (2017), originally published in Scientific Reports (Springer Nature). Used under the terms of the Creative Commons license: https://s100.copyright.com/AppDispatchServlet?title= Seabird%20distribution%20patterns%20observed%20with%20fishing%20vessels%20radar%20reveal%20previously%20undescribed%20sub-meso-scale%20clusters&author=Camille%20Assali%20et%20al&contentID=10.1038%2Fs41598-017-07480-6&copyright=The%20Author%28s%29&publication=2045-2322&publicationDate=2017-08-04&publisherName=SpringerNature&orderBeanReset=true&oa=CC%20BY.

Ashmole, 1971; Goodale *et al.*, 2010). For example, surface feeders can use swimming species to locate a patch but target different individual prey items within the patch, seizing prey near the surface rather than pursuing prey beneath the surface. The result of local enhancement is often that more prey is captured when foraging in conjunction, not less as one would expect for direct competition.

Still, social foraging will not always be beneficial. In little penguins (*Eudyptula minor*), for example, Sutton, Hoskins & Arnould (2015) found that the costs or benefits associated with group hunting depended on prey type. Furthermore, for a patch of a given size there is likely an inflection point for the number of birds at a patch, below which an individual will obtain a benefit from joining the aggregation and above which a bird will experience a cost and should perhaps instead seek a less exploited patch (see Beauchamp, 1998). A recent study demonstrated the utility of using a ship's radar to provide snapshots of the distribution of seabird groups within 30 km of the vessel, updating every few seconds (Assali, Bez & Tremblay, 2017; Assali *et al.*, 2020) (Fig. 8). Future studies may be able to estimate patch quality from such radar images, with large high-quality patches taking longer to deplete and attracting more birds, i.e. with larger echoes that last longer (see Fig. 8). The utility of using the size of seabird echoes as a proxy for patch size can be validated with simultaneous hydroacoustic surveys to capture prey densities or by reviewing video data from birds fitted with cameras foraging within the range of the radar. An important next avenue of research will be to estimate what patches (if any) birds are passing over *versus* foraging at in comparison to all other nearby patch options.

Some studies have investigated the foraging success of individuals as flock size increases. Generally, there is a positive relationship, although positive relationships are more likely to occur in large dispersed patches as aggressive interactions are more common when prey are clumped (Beauchamp, 1998). For Cape gannets, Thiebault *et al.* (2016) observed the lowest attack success rate when individuals dived alone, i.e. with no other birds diving in the previous 15 s, and success rate was maximised when a gannet dived in the presence of two other diving gannets. Even dives in the presence of 20 or more others were more successful than solo dives. Similarly, an experiment by Gotmark *et al.* (1986) found that the number of fish obtained by black-headed gulls was higher for birds in flocks of six than in flocks of three, and higher for flocks of three than for solo birds.

It is of concern that anthropogenic changes may be altering the quantity and quality of beneficial species interactions, with fitness consequences for those involved (Fig. 7). In this era of global change we are challenged with the task of maintaining critical ecosystem functions and services, and diversity metrics other than species richness are increasingly recognised as playing key roles. It may be important to conserve groups of species that facilitate one another as units of biodiversity (Greggor *et al.*, 2017; Veit & Harrison, 2017; Monier *et al.*, 2020). This likely involves reexamining species interactions previously assumed to be competitive for evidence of mutualisms and facilitation.

VI. CONCLUSIONS

(1) Seabirds are notably absent from the cognition literature, despite the fact that seabirds exhibit many behaviours that promote learning and the transmission of information between individuals (see examples in Table 1). They deserve more attention in this regard. To my knowledge, this is the first review dedicated to the foraging cognition repertoire of seabirds. While the focus of this review falls on their social foraging skills and behaviours, social information use is a major strategy for seabirds to find food. This may have been underestimated previously because of presumed competitive costs, and because of the difficulty of observing birds at sea where many of these interactions occur. This review describes under what circumstances the benefits of social foraging interactions can outweigh the costs.

(2) Social cues provide seabirds with updated information about the location of prey and, once at a patch, facilitation often occurs that can provide benefits. Local enhancement is often opportunistic (birds move towards others when they see them) and information is transferred passively (feeding flocks are public information). Penguins are notable for their apparent coordination while foraging, but evidence for such behaviours in other seabirds is lacking. This may be, in part, due to the difficulty of obtaining evidence for such interactions observationally at sea, and therefore future work should test the limits of seabirds' capacity for cooperation experimentally.

(3) Despite social information use being common amongst seabirds, the extent to which seabirds forage socially *versus* solitarily varies considerably within and across species. Importantly, the distribution of costs/benefits may not be equal across all members of a flock, and the nature of these species interactions is not fixed. It has been proposed that the poor foraging skills of young individuals contributes to the high juvenile mortality rate of seabirds (MacLean, 1986; Riotte-lambert & Weimerskirch, 2013), and thus a thorough understanding of how such skills are acquired and utilised would benefit future conservation efforts. While positive relationships between foraging efficiency and age have been documented, future studies should design experiments to provide direct evidence for the development of socio-cognitive skills as the mechanism involved. The extent to which species or individuals are reliant on social cues *versus* can flexibly deploy other search strategies (Fig. 1) should be quantified, as the ability to switch between search strategies could help buffer against environmental change (i.e. what is the magnitude of link d in Fig. 7?).

(4) The negative effects of competition at a patch may be countered (or outweighed) by the presence of those competitors facilitating patch discovery *via* local enhancement. Additionally, different species of marine predators join feeding

flocks at different stages of their formation and exhibit different prey-capture strategies and there is evidence that the presence of these different behavioural phenotypes enhances prey-capture success. For a patch of a given size there is likely an inflection point regarding the number of birds present, below which individuals benefit from joining the aggregation and above which the birds experience a cost and should instead seek a less-exploited patch. Investigating this will require the simultaneous tracking of seabirds and their prey. Such studies are now possible as the associated technology has become less expensive and less computationally demanding.

(5) It is clear that social interactions are an integral component of seabird foraging behaviour. It has been demonstrated empirically these interactions are positively linked to fitness proxies such as increased patch detection and decreased search time. Social foraging can also enhance prey capture, and the presence of others at a feeding site has been shown to reduce neophobia and latency to feed. Future work must now assess direct fitness benefits, by measuring how social foraging is related to factors such as clutch size, fledgling success, and lifetime reproductive success.

VII. ACKNOWLEDGEMENTS

Support for this work was in part provided by U.S. National Science Foundation Office of Polar Programs grant 2011454, by the College of Staten Island Biology Department and the Division of Science and Technology, and by a the City University of New York Graduate Center Fellowship and Doctoral Student Research Grant. I thank Richard R. Veit, David Lahti, Lisa Manne, Jarrod Santora, Shaibal Mitra, and Philip Johns for fruitful discussions and thoughtful feedback.

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(*Received 11 April 2023; revised 11 April 2024; accepted 15 April 2024; published online 2 May 2024*)