

Group-foraging and information transfer in European shags *Phalacrocorax aristotelis*

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Abstract

Many animals including marine mammals and several seabird species dive in large groups, but the impacts that social interactions can have on diving behaviour are poorly understood. There are several potential benefits to social diving, such as access to social information or reduced predation risk. In this body of research I explore the use of social information by groups of diving animals by studying the behaviour of European shags (*Phalacrocorax aristotelis*) diving in “foraging rafts” in the Isles of Scilly. Using GPS tracking I establish where shags regularly forage in relation to bathymetry and areas where foraging rafts frequently formed. Using these data I show that the foraging ranges of different colonies overlap and that foraging ranges of individual shags are often predictable. This suggests that social information will be of less value while searching for foraging patches. However, using observational studies to further explore the conditions and areas in which foraging rafts formed, I show that advantages such as anti-predation or hydrodynamic benefits are unlikely to be the main drivers of rafting behaviour in the Scillies. I therefore suggest that access to social information from conspecifics at a foraging patch may be one of the main benefits diving in groups. Using a dynamic programming model I show that individuals diving in a group benefit from using social information, even when unable to assess conspecific foraging success. Finally I use video analysis to extract the positions and diving behaviour of individuals within a foraging raft and compare this to simulated data of collective motion and diving behaviour. The results of these studies indicate that an individual being able to utilise dives of conspecifics to inform their own diving decisions may be one of the main advantages of social diving.

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Chapter 2

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1. General Introduction



1.1 Information use

All animals are constantly faced with uncertainty while making decisions. When deciding how to move, forage, breed or avoid predation an animal must consider the behaviour of other animals, the current state of their environment and how that environment might change. As making an incorrect choice could result in injury, missed opportunities, starvation and death, making informed decisions will be enormously important (Dall *et al.*, 2005a). As such, animals must constantly strive to reduce uncertainty by gathering information (defined here as anything that leads to any reduction of prior uncertainty (of an evolved receiver) that improves its functioning (Schmidt, Dall & Van Gils, 2010b)) in order to make optimal decisions. The need to acquire information therefore pervades many aspects of animal behaviour and is recognised as an important resource for animals (Dall *et al.*, 2005a; McNamara & Dall, 2010b; Schmidt *et al.*, 2010b).

There are several different ways animals can gain information. When alone, animals can rely on their prior experience while making decisions or attempt to acquire information, either from environmental cues or through trial and error (Dall *et al.*, 2005a). For example, an animal might estimate its predation risk based on cues of predator activity, the level of cover in an area or simply by the fact it has not previously been killed while foraging in that area. Similarly, while foraging an animal might use their previous experience to decide where and on what to forage, but might also sample the environment to assist in deciding where to forage (Dall *et al.*, 2005a; McNamara & Dall, 2010b). However, such *personal information* can rapidly become outdated and animals are therefore required to sample their environment on a regular basis in order to ensure they are still making the correct decisions (Laland, 2004). This requires

an animal to spend time and energy gathering information as well as potentially facing increased risks while doing so (Dall *et al.*, 2005a). A large amount of work has been carried out examining the trade-off between the need to maintain up to date information with other biological needs (Dall *et al.*, 2005a; McNamara & Dall, 2010a; Schmidt *et al.*, 2010b). Particular attention has been given to how animals must assess their own foraging success so as to make the decisions that will maximise intake (optimal foraging (McNamara & Houston, 1985; Pyke, 1984; Wajnberg *et al.*, 2006)).

While animals can acquire a great deal of information simply through trial and error, they can also monitor the behaviour of other animals to assist in making their own decisions. Using this *social information* is often considerably less costly than an individual attempting to gather personal information themselves by assessing the environment (Dall *et al.*, 2005a; Valone, 2007). This can be shared “intentionally” through the use of signals, whereby animals use certain behaviours or traits that have been selected directly to share information. These can range from an animal broadcasting their fitness to prospective mates to signalling the presence of a predator with alarm calls. The use of signals is particularly common in highly social species, which often deliberately alert other group members to the presence of food or predators (Graw *et al.*, 2014; Wright *et al.*, 2001). Alternatively, animals can also generate social information completely inadvertently, which other animals can benefit from. The mere presence of conspecifics or heterospecifics with similar resource needs might provide an indication of resource availability, as well as resource quality (Dall *et al.*, 2005b; Danchin *et al.*, 2004). There are also numerous behaviours that might give detailed information to any observing animals, such as a conspecific successfully capturing prey or achieving high

breeding success in a particular area. The use of this type of information can be thought of as a form of “information parasitism”, where one individual actively produces information while another scrounges it at little cost. While allowing other individuals to take advantage of this information may not be beneficial to the producer, it is usually simply too difficult and costly to attempt to actively hide this information from conspecifics (Valone, 1989). Numerous studies have shown how access to social information can enhance an animal’s predator detection rates, reproductive success and foraging efficiency (Boulinier *et al.*, 2008; Campobello & Sealy, 2011b; Danchin *et al.*, 2004; Weimerskirch *et al.*, 2010). Many of these have been focused around the use of information by animals living in groups, examining how the use of social information affects the behaviours and decision making of individuals within the group. Better decision making due to easy access to social information has been suggested as one of the primary advantages of group living (Valone, 2007).

1.2 Social information in colonial species

Of the many types of grouping behaviour, colonial breeding and colonial roosting have received particular attention. Colonial animals aggregate to breed or roost in territories with no defendable resources, well above densities predicted by the ideal free distribution (Fig. 1). The individuals within the colony do not display a high level of relatedness, as opposed to the individuals in eusocial colonies (Danchin & Wagner, 1997; Forbes & Kaiser, 1994; Kildaw, 1999; Olsthoorn & Nelson, 1990; Rolland, Danchin & de Fraipont, 1998). Despite the large body of work studying coloniality and the frequency of the behaviour across a wide range of species (Armitage, 1962; Riedman, 1990; Trillmich & Trillmich, 1984; Uetz *et al.*, 2002) no clear answer as to the origins and advantages of coloniality has been established. One suggestion is that

social information transfer at the colony is one of the main drivers of coloniality. The most prevalent information based hypothesis is that colonies act as information centres for the transfer of foraging information (Bijleveld *et al.*, 2010; Ward & Zahavi, 1973a). In order for this to work, numerous requirements must be met. Prey must be patchy and ephemeral, but last long enough that an individual can make at least one return trip. Animals at the colony must be able to assess the success of a returning individual so as to choose a successful individual to follow back to a patch. Upon reaching a patch, prey must also be abundant enough that competition isn't an issue. Following an informed individual must improve the foraging success of an unsuccessful individual and any differences in individual success must be due to chance or individual's ability to locate prey, not because of differing abilities to exploit food patches (Ward & Zahavi, 1973a).

These requirements have proven difficult to test empirically, and studies have struggled to produce evidence for the hypothesis. This has led to the information centre hypothesis (ICH) generating a great deal of debate (Danchin & Wagner, 2001; Mock, Lamey & Thompson, 1988; Richner & Heeb, 1995; Richner & Danchin, 2001). Much of the criticism has been drawn by the apparent need for active signalling to take place at the colony, which is difficult to justify in non-related individuals without resorting to reciprocal altruism. While this can be explained via returning individuals generating inadvertent information (especially in breeding colonies where it is possible to observe successful animals feeding their young) and "subtly guiding" uninformed individuals with their directions of travel (Couzin *et al.*, 2005), it has led to the development of an alternative theory: the recruitment centre hypothesis (RCH, Richner & Heeb, 1996). This idea states that animals will gain an advantage at

a patch when foraging in a group. It is therefore advantageous for an informed individual to return to a colony to recruit conspecifics to feed. This avoids the apparent need for group selection present in the ICH (Danchin & Wagner, 1997; Richner & Heeb, 1996).

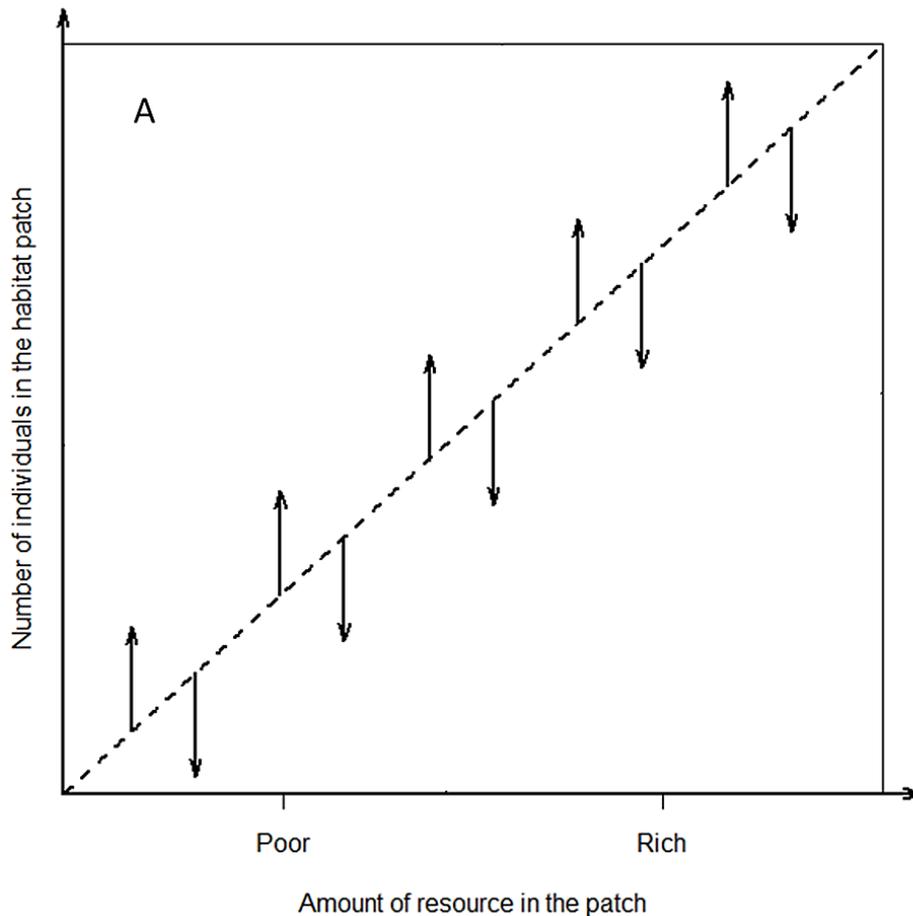


Figure 1.1: The ideal free distribution, represented by the dashed line which predicts that animals will distribute themselves to match the distribution of resources among patches. Deviating from this leads to over and underexploited areas, represented by vertical arrows. Patches below the line are under exploited, while patches above the line are over exploited. Aggregations are greater as vertical distance above line (as shown by arrows) increases. Colonially breeding species breed in areas of highest overexploitation: A, leaving many potential territories unoccupied (Fretwell & Lucas, 1969; Olsthoorn & Nelson, 1990). Figure adapted from Danchin, Giraldeau and Cézilly (2008).

While compelling, the RCH has proven equally difficult to test empirically (Danchin & Wagner, 2001; Marzluff & Heinrich, 2001; Mock, 2001; Richner & Danchin, 2001). Much of the work examining these hypotheses has been carried out on seabirds, as many of these species meet the requirement of feeding on patchy and ephemeral prey, making foraging information extremely valuable. Unfortunately these (ideal) properties also make it extremely difficult to acquire data on their behaviour, especially their behaviour at the patch. Recently however, advancements in GPS technology and miniaturisation of cameras have allowed us to gain a great deal of detailed information about the movements and behaviours of birds at sea, providing insight into the use of information (Burger & Shaffer, 2008).

1.3 Information use at the patch and diving

While the recruitment centre hypothesis suggests there may be an advantage to foraging in a group, it does not specify what that advantage may be. In order for recruiting others to feed to be a viable tactic, the advantages gained must be greater than the disadvantages an individual will incur while foraging in a group. Animals within a foraging group will face increased competition (Foster, 1985; Ranta, Rita & Lindstrom, 1993), interference (Ruxton, 1995) and conspecific kleptoparasitism (Ranta *et al.*, 1993). Large groups can also attract heterospecific kleptoparasites and predators (Cresswell, 1994). Potential benefits that outweigh these costs include reduced individual risk (Roberts, 1996), enhanced predator detection (Beauchamp, 2001; Cresswell, 1994), resource access (Dall & Wright, 2009a) and increased foraging intake due to easy availability of social information (Dermody, Tanner & Jackson, 2011; Templeton & Giraldeau, 1995) or better ability to capture prey (Bednarz, 1988; Handegard *et al.*, 2012).

While all of these advantages might lead terrestrial colonial species to recruit conspecifics to forage, as discussed above much of the research examining recruitment centres and information centres has been carried out on colonial seabirds. Animals engaging in group foraging in marine or aquatic systems are likely to be subject to an entirely different set of restrictions and pressures. The need for animals feeding in these environments to hold their breath while finding, pursuing and catching their prey may fundamentally alter the costs and benefits of foraging in a group. Additional advantages may include being able to enhance foraging efficiency by reducing the energetic costs of diving through hydrodynamic benefits (Noren, Biedenbach & Edwards, 2006) or by engaging in coordinated prey herding behaviour (Battley *et al.*, 2003; Benoit-Bird & Au, 2009). Diving animals could also benefit substantially from increased access to social information. A dive involves a significant investment in time and energy (Williams & Yeates, 2004), meaning that making an informed dive is extremely important for maximising foraging efficiency. This is especially important as keeping track of the distribution of underwater prey can be extremely challenging, depending on the clarity of the water and the visual capabilities of the animal (Machovsky-Capuska *et al.*, 2012; Stempniewicz *et al.*, 2013; Strod *et al.*, 2008; White *et al.*, 2007). Reducing uncertainty about where prey is underwater before diving, via social information from conspecifics, could therefore be extremely beneficial to animals attempting to optimise diving behaviour.

It is important to distinguish between the different kinds of aggregations group diving animals can form. Large chaotic assemblages of seabirds frequently form due to conspecific attraction or local enhancement. These usually occur simply because all individuals are trying to exploit the same food

source and tend to be disorganised with a high degree of intraspecific kleptoparasitism taking place (Barnard, Thompson & Stephens, 1982; Hoffman, Heinemann & Wiens, 1981). This is different from social diving in which conspecifics form highly organised groups, displaying a high degree of alignment, polarity and synchronicity of diving (Beauchamp, 1992; Berlincourt & Arnould, 2014; Saino, Fasola & Waiyakp, 1995; Schenkeveld & Ydenberg, 1985b; Tremblay & Cherel, 1999). This type of formation can be found in surf scoters (*Melanitta perspicillata*) (Lukeman, Li & Edelstein-Keshet, 2010b), Barrow's goldeneyes (*Bucephala islandica*) (Schenkeveld and Ydenberg 1985; Beauchamp 1992), American White Pelicans (*Pelecanus erythrorhynchos*) (Anderson 1991) and numerous related Phalacrocorax species (Nelson, 2005). These differ from other aggregations, such as the compass rafts Guanay cormorants form near colonies (Weimerskirch, Bertrand et al. 2010), the rafts several species of seabirds form near colonies (Wilson, McSorley et al. 2009) or the rafts waterfowl species form (Fox, Green et al. 1994; Fox and Mitchell 1997). Little to no diving occurs within these rafts, with the main activities being sleeping, preening or waiting to return to nests at nightfall (Furness, Hilton et al. 2000; Wilson, McSorley et al. 2009).

The coordination observed during this social diving must bring additional benefits, compared to every individual trying to access prey at the same time, in order for these types of assemblages to be useful. It is likely that some of the benefits mentioned above such as anti-predation benefits, prey herding or reduced diving costs due to hydrodynamic benefits require the degree of coordination seen in these groups.

1.4 Study System

Observations were carried out on European shags *Phalacrocorax aristotelis* (hereafter 'shag'). Shags and cormorants (Family: *Phalacrocoracidae*) are colonial breeding, inshore pursuit diving seabirds consisting of around 40 species that breed at high latitudes in both hemispheres as well as in tropical waters (Nelson, 2005). European shags breed around the Atlantic and Mediterranean coasts of Europe and typically forage in sandy, rocky areas at depths of up to 60 metres, mainly on small fish, supplemented by crustaceans (Nelson, 2005). Shags can also engage in group foraging behaviour, forming large rafts, often consisting of long belts of several hundred individuals moving along the surface of the water and diving together, displaying a high degree of cohesion and alignment (Nelson, 2005). While in these assemblages birds will regularly "leap frog" each other, with birds from the back flying to the front of the group where they immediately begin diving, which may provide foraging benefits such as an increased intake for individuals or some form of fish-herding (Anker-Nilssen, 2009). Similar behaviours can be found in several other *Phalacrocorax* species around the world (Nelson, 2005). Though foraging rafts have been observed in numerous locations, they appear to form most frequently in proximity to large colonies (Anker-Nilssen, 2009; Velando & Munilla, 2011).

The population of shags studied was based on the Isles of Scilly (49.9361° N, 6.3228° W). This archipelago consists of five inhabited islands and roughly 300 rocks and uninhabited islands. The islands are a Special Protection Area under EU law, in part because of the seabird assemblage of international importance (Heaney *et al.*, 2008). Approximately 20,000 seabirds, of 13

different species breed within the islands, including ~1300 breeding pairs of shags (Heaney *et al.*, 2008).

1.5 Thesis outline

Chapter two reviews the numerous way in which information can be used in colonially living animals. I address how social information from conspecifics within a colony can aid animals in making decisions about avoiding predators, reducing brood parasitism, migratory phenology, mate choice, habitat choice and foraging. This chapter also discusses how the use of social information can lead to the development and maintenance of colonies and demonstrate the ubiquity of information for colonially living species.

Chapter three investigates the movement and foraging behaviour of individual shags from multiple colonies within the isles of Scilly using bird-borne GPS devices. The areas where these birds foraged were compared to datasets of observations of foraging rafts and bathymetry. Birds were found to have short, overlapping foraging ranges with no clear differences between colonies. All birds foraged mainly in the shallow waters between islands. While these patterns suggest make it unlikely that shags engage in information transfer at the colony, I suggest that the high degree of overlap may be related to social diving behaviour.

Chapter four examines how environmental conditions affect the formation and distribution of foraging rafts within the Isles of Scilly in order to gain insight into the types of advantages gained by diving within such an assemblage. Shore-based observations revealed that raft size is influenced by changes in tide and sea state. The conditions and areas in which rafts form appear to rule out advantages such as hydrodynamic benefits or coordinated fish herding and

lend extra weight to the idea that the easy availability of social information in order to enhance foraging efficiency may be one of the main advantages to diving in a group in this system. Chapter five explores the logic of this idea with a dynamic state variable model, investigating the value of copying the diving decisions of conspecifics as a foraging strategy, in relation to environmental conditions and group size. This chapter demonstrates the benefit of copying the dive behaviour of neighbours and using conspecifics to find and keep track of prey below the surface. Copying dive behaviour was found to be optimal, even when an animal was unable to judge the foraging success of conspecifics accurately.

In Chapter six a combination of group motion analysis and simulated models of zonal interaction are used to investigate the behaviour of socially diving individuals. In order to ascertain the level of social information use within foraging rafts I test which models of individual movement and diving behaviour best fit the movement and diving behaviour extracted from video data of groups of shags. The results found suggest that shags use the diving behaviour of their conspecifics to inform their own dive decisions, corroborating the notion that this may be one of the main advantages of social diving behaviour. The wider implications of this finding and the findings of previous chapters are discussed in Chapter seven, where I also suggest ways in which the use of information in diving animals could be studied further.

2. Information use in colonial living



2.1 Abstract

Despite the fact that many animals live in groups, there is still no clear consensus about the ecological or evolutionary mechanisms underlying colonial living. Recently, research has theorised that colonies may be important as sources of social information. The ready availability of information from conspecifics allows animals to make better decisions about avoiding predators, reducing brood parasitism, migratory phenology, mate choice, habitat choice and foraging. These choices can play a large part in the development and maintenance of colonies. Here we review the types of information provided by colonial animals and examine the different ways in which decision-making in colonies can be enhanced by social information. We discuss what roles information might take in the evolution, formation and maintenance of colonies. In the process, we illustrate that information use permeates all aspects of colonial living.

2.2 Introduction

Coloniality is prevalent across a wide variety of taxa including both terrestrial and marine mammals, birds, reptiles and spiders (Armitage, 1962; Riedman, 1990; Trillmich & Trillmich, 1984; Uetz *et al.*, 2002). In birds alone, coloniality has been shown to have evolved independently at least twenty times, with up to 19% of species breeding in colonies (Crook, 1965; Rolland *et al.*, 1998). However, despite a large number of plausible hypotheses and several theoretical and empirical studies examining the issue, there remains no consensus about the evolution of coloniality (Danchin *et al.*, 2008). Here we interpret coloniality as when animals aggregate to breed well above densities predicted by the ideal free distribution (where animals distribute themselves to match the distribution of resources among patches: Fretwell & Lucas, 1969) in

territories that contain no defensible resources, leaving many other potential territories unoccupied (Danchin & Wagner, 1997; Forbes & Kaiser, 1994; Kildaw, 1999; Olsthoorn & Nelson, 1990; Rolland *et al.*, 1998). These animals often do not show high levels of relatedness, with pairs breeding independently, unlike eusocial colonies (Kerth, Safi & König, 2002; Reeve *et al.*, 1990; Wilmer *et al.*, 2000). This occurs in spite of several obvious evolutionary disadvantages of group-living such as increased competition for resources, cuckoldry and transmission of disease and parasites (Brown & Brown, 1986; Hoogland & Sherman, 1976; Møller, 1987; Péron, Lebreton & Crochet, 2010). There must therefore be advantages to coloniality that outweigh the potential fitness costs.

We suggest that almost all potential advantages of colonial breeding must involve some level of enhanced information use, even if most of the original hypotheses (e.g. coloniality enhancing predator defence or reproductive success, see Fig. 2.1) do not explicitly state this. For animals living in groups, the transfer of information is inescapable due to the cost and difficulty of hiding information from conspecifics (Valone, 1989). As such, it may provide a useful framework for increasing our understanding of the mechanisms behind coloniality (Boulinier & Danchin, 1997). Information is increasingly recognised to be important for animals, allowing them to reduce uncertainty in order to improve decision making in the face of changing ecological circumstances (Dall *et al.*, 2005b; Danchin *et al.*, 2004; McNamara & Dall, 2010a; Schmidt *et al.*, 2010b). Gathering information via personal trial and error can be costly; it can therefore sometimes be more cost effective to gather social information from conspecifics, either from deliberate signals or via inadvertent social information generated by their activities (Dall *et al.*, 2005b). For example, the presence of conspecifics or heterospecifics can provide information on resource availability,

as well as resource quality (Dall *et al.*, 2005b; Danchin *et al.*, 2004).

Aggregations of conspecifics will produce increased opportunities for the acquisition of social information (Danchin *et al.*, 2004; Valone, 1989). As such, information will play an important role for animals living in colonies, and several influential hypotheses about the advantages of coloniality have been based on information transfer assisting in certain decisions (Boulinier *et al.*, 1996; Forbes & Kaiser, 1994; Ward & Zahavi, 1973a).

In this review we examine the different types of information that can be shared among individual animals that breed in colonies or roost communally. This includes theoretical and empirical behavioural studies on how colonies influence decisions about predators, foraging, habitat, mates and other key socio-ecological factors. Also reviewed are evolutionary studies demonstrating how information use could have led to the evolution of coloniality. It is important to make a distinction between colonial breeding and nesting, as opposed to colonial roosting. We define colonial breeding as two or more individuals breeding together in a site containing no resources other than the breeding patch itself (Meadows *et al.*, 1972), while in colonial roosts, individuals aggregate to rest (Beauchamp, 1999b). Unlike breeding colonies, communal roosts may vary in time and space more than breeding colonies due to the presence of eggs or young at the latter, and as such will be subject to different evolutionary pressures (Caccamise & Morrison, 1986). Communal roosts also tend to be more transitory in both membership and spatial location (Caccamise & Morrison, 1986; Heisterberg *et al.*, 1984) while breeding colonies tend to be more stable (Meadows *et al.*, 1972), although this is not always the case (Burger, 1984; Kotliar & Burger, 1986; Montevecchi, 1978). Both may utilise the same sites over multiple generations (Marshall, 1983; Oro & Pradel, 2000;

Porter & Coulson, 1987). The current review focuses on colonial breeding but studies of communal roosts provide important evidence for the significance of information use, to which we will refer.

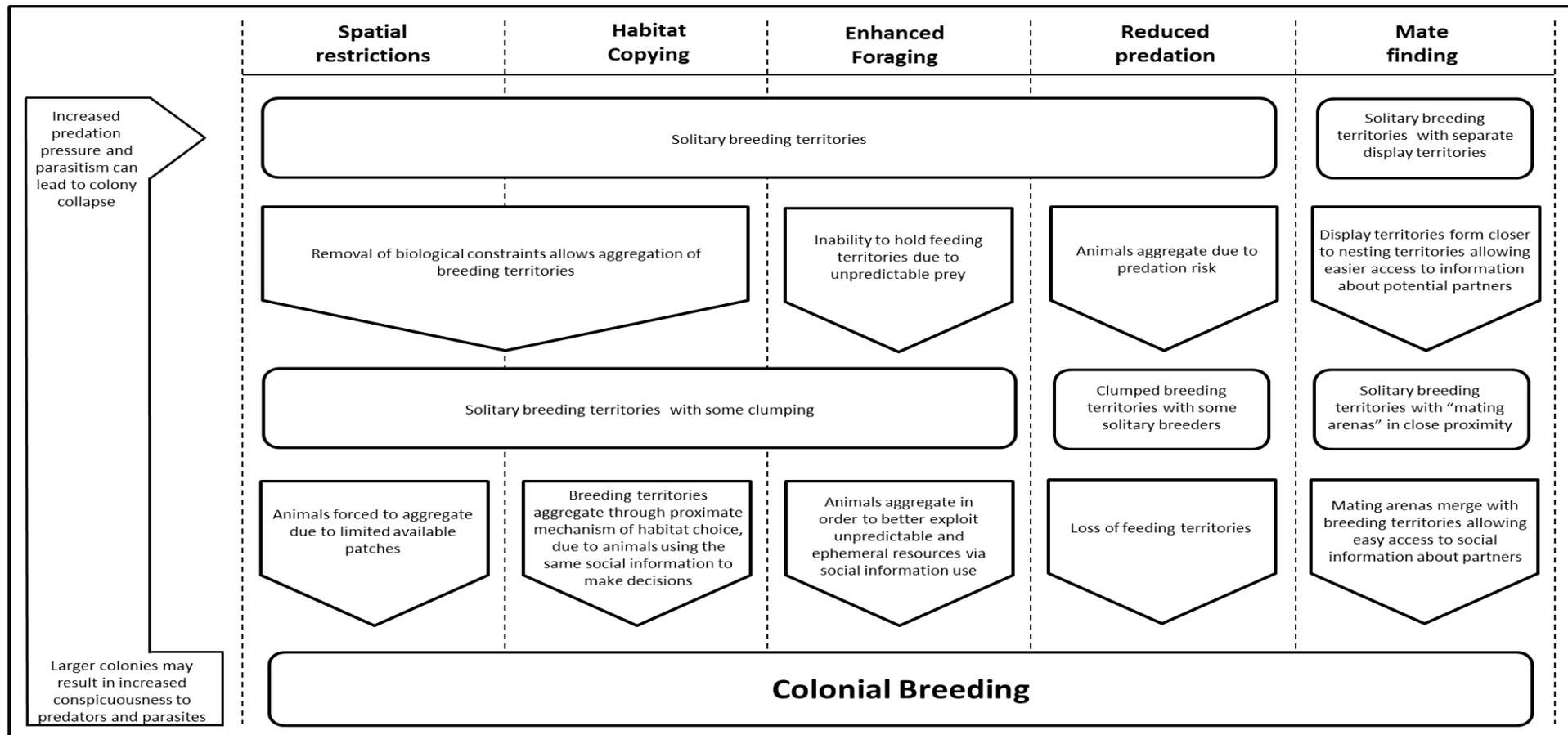


Figure 2.1: Potential evolutionary pathways to colonial breeding. Removal of biological constraints refers to evolutionary changes that allow animals to aggregate, such as a general inability to hold breeding territories, increased tolerance of conspecifics or an environmental change that forces aggregation (See: Rolland *et al.* (1998)). How prevalent clumped breeding territories are in the second stage will likely vary depending on species and situation. In this case we assume that under predation risk clumped breeding territories will become more common faster. Though the loss of feeding territory is common in many colonial species, there are likely exceptions (See section 7.6)).

2.3 Information for predator defence

One of the earliest proposed drivers for the evolution of colonial breeding is the reduction in an individual's susceptibility to predation (Darling, 1938) and several studies have found an increase in both survival and reproductive success in colonies as group size increases (Barbosa *et al.*, 1997; Hoogland & Sherman, 1976; Hoogland, 1981). Some of these may be explained by the presence of a large number of animals causing dilution and satiation effects (collectively referred to simply as passive group size effects) or confusion effects (which can be either a passive effect or an active group defense, Handegard *et al.*, 2012; Ims, 1990; Inman & Krebs, 1987; Krakauer, 1995; Krause, 2005; Miller, 1922; Will, 1994). Nevertheless, how compelling is the evidence that such non-informational forms of predator defence are important evolutionary drivers of coloniality?

Greater levels of survival and reproductive success in the centre of colonies have been reported in a variety of species (Hoogland, 1981; Liljeström *et al.*, 2008). Similarly, comparative studies in species which breed both solitarily and colonially have found reduced predation and increased reproductive success in animals that chose to nest in breeding colonies (Götmark & Andersson, 1984; Neff, Cargnelli & Côté, 2004; Sasvári & Hegyi, 1994). Despite these potential advantages, several studies actually report a higher predation rate per capita in larger colonies, or no effect of increased colony size (Brunton, 1997; Burger, 1974; Picman, Pribil & Isabelle, 2002; Pienkowski & Evans, 1982). While coloniality may initially decrease individual predation risk via passive group size effects, as colony size increases this may, in some instances, be offset by the greater conspicuousness of the group causing an increase in net predation rates (Clode, 1993; Varela, Danchin & Wagner, 2007). It has thus been suggested that colonies would evolve toward an intermediate

colony size, large enough to provide maximum anti-predation benefits but small enough to avoid attracting predators (Brown, Stutchbury & Walsh, 1990). Few studies show that intermediate sized colonies are most successful (Serrano *et al.*, 2005; Wiklund & Andersson, 1980), likely due to the evolutionary instability of “optimal” group sizes (Brunton, 1999; Pulliam & Caraco, 1984; Sibly, 1983) and the difficulty of sampling a sufficient range of colony sizes (Brown, 1996; Brunton, 1999; Serrano *et al.*, 2005). Stable colony size will also vary depending on the environmental conditions and predators present (Brunton, 1999; Wiklund & Andersson, 1994). For example, a study of fieldfare *Turdus pilaris* colonies in Sweden found that in the north, colonies were larger for likely due to enhanced predator defence. However in the south the presence of tawny owls *Strix aluco*, which were attracted to large noisy colonies, led to significantly smaller colonies (Wiklund & Andersson, 1994). This will also be the case if predators learn to specialise on the rich sources of prey that colonies represent (Brunton, 1997; Larivière & Messier, 1998; Oro, 1996; Picman *et al.*, 2002; Varela *et al.*, 2007; Votier *et al.*, 2007). In these situations, if a colony does provide anti-predation benefits, it must do so in other ways, such as by providing easy access to information about potential threats.

2.3.1 Vigilance in colonies and perceived predation risk

Large numbers of conspecifics breeding in close proximity can utilise the alarm signals and behaviour of others within the colony as sources of social information about predation risk (Danchin *et al.*, 2004; Robinson, 1985). This can give colonies an increased probability of early predator detection. For example, in a study of cliff swallows *Hirundo pyrrhonota* it was found that predator detection distance increased with colony size (Brown & Brown, 1987). Such collective

detection is especially important in breeding colonies where there are a high proportion of vulnerable young. The easy availability of such social information and/or passive group size effects can allow individuals to reduce the amount of time they spend vigilant without reducing the group's overall probability of predator detection (Danchin *et al.*, 2004; Klose *et al.*, 2009). Many studies examining vigilance in groups have found this relationship between group size and individual vigilance (Barbosa *et al.*, 1997; Elgar, 1989; Fernández, Capurro & Reboreda, 2003; Gilbert, 1995). As well as reducing mortality risk, reduced vigilance would allow more time to be spent on other activities such as preening, courting or care of young (Elgar, 1989; Picman *et al.*, 2002).

While such changes in vigilance have been studied in various group types (Rieucou, Morand-Ferron & Giraldeau, 2010; Sansom *et al.*, 2008), individual alertness has been examined at the colony level relatively rarely. Some studies initially aimed to examine alertness within colonies, but this was constrained by the difficulty of monitoring individuals (Brown & Brown, 1987). However, reduced individual vigilance in larger colonies has been observed in American cliff swallows *Petrochelidon pyrrhonota* and in mixed colonies of lesser kestrels *Falco naumanni* and jackdaws *Corvus monedula* (Campobello, Sarà & Hare, 2012; Roche & Brown, 2013). Reduced vigilance has been found in larger colonies of prairie dogs *Cynomys ludovicianus*, but further studies of a related species *Cynomys gunnisoni* suggested that vigilance decreased with colony size only in small colonies (Hoogland, 1979; Verdolin & Slobodchikoff, 2002). Monitoring group size may be more difficult in colonies than other forms of group living, as many colonies are found in environments, such as cliffs (Roche & Brown, 2013) or flat topped rocky islands (Good, 2002) that make it harder for animals to monitor conspecifics. This is

especially the case if an animal chooses a visually obscured nest site (García-Borboroglu & Yorio, 2004; Good, 2002) or colonies are comprised of burrows (Hudson, 1982; Nico, Jelks & Tuten, 2009). As a colony grows, it becomes increasingly difficult for individuals to monitor its size, meaning that perceived risk is more likely to be affected by local neighbours than the entire colony. As such, the benefit of information on predation risk will not increase above a certain colony size. Similarly this information will be less easily available in colonies with more complicated spatial structures.

2.4.2 Information when reacting to predators

While passive group size effects and collective detection are not mutually exclusive, the importance of collective vigilance versus changes in perceived risk caused by passive group size effects in causing reduction in vigilance varies among and within species (Beauchamp & Ruxton, 2008). Some species choose to flee to avoid predation (Clode, Birks & Macdonald, 2000; Danchin *et al.*, 2004). This behaviour often takes the form of an information cascade where the fleeing behaviour of one individual acts as a social information cue causing many others to adopt the same behaviour, even if the initial flight response was in error (Giraldeau, Valone & Templeton, 2002). Such a mass exodus does have the advantage of conferring extra protection to fleeing individuals via passive group size effects (Jeschke & Tollrian, 2007; Krakauer, 1995; Ruxton, Jackson & Tosh, 2007). However while a flee response reduces the chances of adult predation, it leaves nests vulnerable (Giraldeau *et al.*, 2002). Alternatively animals can engage in group defence. This can take two forms. Indirect group defences such as aggressive displays or direct group defence such as body striking or swooping (Clode *et al.*, 2000; Kazama & Watanuki, 2010). Group defence effectiveness is increased in

larger colony sizes due to the larger number of individuals to contribute to defence (Krams, Bērziņš & Krama, 2009). A large number of individuals mobbing a predator will also cause significant confusion, reducing lethality. This, and the greater numbers present in large colonies, allows animals to reduce their individual risk while engaging in direct defence, increasing their likelihood of participating (Arroyo, Mougeot & Bretagnolle, 2001).

While in the past it has been assumed that individuals in a targeted area will contribute equally to group defence due to shared predation risk, it has been shown that different colony members adopt different strategies based on information available, perceived risk and individual differences (Kazama & Watanuki, 2010; Kazama *et al.*, 2011). Some of these individual differences are stable, with consistently aggressive individuals reliably contributing intensively to group defence. Many other individuals will flee or attack predators more selectively. Different predators provoke different levels of direct defence or flee response, depending on an individual's perceived risk to themselves and their offspring (Clode *et al.*, 2000; Kazama *et al.*, 2011). Information on the nature of an attacking predator is required to decide which strategy to utilise. If an animal has never encountered a particular predator before, monitoring the behaviour of other more experienced individuals within the colony can act as a cue allowing them to refine their strategy and decide how much effort to place in defence. Even experienced individuals can still utilise the intensity of a neighbour's defence as a reliable indicator of predator threat when deciding what strategy to adopt (Danchin *et al.*, 2004; Kazama & Watanuki, 2010; Kazama *et al.*, 2011). Black tailed gulls *Larus crassirostris* and tree swallows *Tachycineta bicolor* will alter the effort invested in defence based on cues from their neighbours (Brown & Hoogland, 1986; Kazama *et al.*, 2011; Winkler, 1992).

Conversely, other species such as Montagu harriers *Circus pygargus* reduce individual investment as more neighbours participate and increased conspecifics at the colony compensates for reduced individual effort (Arroyo *et al.*, 2001).

2.4.3 Predation and the evolution of coloniality

The effect of coloniality on predation clearly goes beyond simply lowering of individual risk due to passive group size effects. Animals can utilise colonies as a source for a wide variety of information that they can use to further reduce their predation risk or make decisions on how to react to predators. There remain however, several unanswered questions about which cues are used and how that information is utilised. The question also remains, how important are these anti-predation benefits for the evolution of colonial behaviour and the formation of colonies? For example; in the case of avian coloniality, if colonial living provided sufficient protection from predators, solitary species with vulnerable nests would be more prone to evolve to become colonial, while the nests of species already breeding in colonies would evolve to be more vulnerable (Varela *et al.*, 2007). However a comparative phylogenetic analysis of *Ciconiiformes* found that colonial species with vulnerable nests were more likely to (i) evolve protected nests than solitary species, and (ii) evolve to become solitary than colonial species with protected nests (Varela *et al.*, 2007). This appears to show that coloniality increases vulnerability suggesting that across evolutionary time, coloniality has provided little protection from predators in *Ciconiiformes*.

Predation may therefore be unlikely to be a major selective pressure driving coloniality. Alternatively, while predation might have been an initial driver of coloniality, the evolutionary arms race between predators and prey may have

reduced anti-predation benefits over time. Similarly, if anti-predatory advantages were the main force in the evolution of coloniality (Fig. 2.1), we might not expect coloniality to evolve in large aggressive species such as raptors, though studies have shown that these species still suffer significant egg and young predation (Sarà, Campobello & Zanca, 2012; Varela *et al.*, 2007). If coloniality does confer anti-predation benefits then colonial birds might be expected to produce larger clutch sizes due to increased survival rates. Once again, the decrease in predation risk observed in many of the previously mentioned studies fails to translate into significant evolutionary change, as clutch sizes have not been found to be larger in colonial species (Beauchamp, 1999a). This may be because due to higher rates of ectoparasitic infection in colonial species (Brown & Brown, 1986; Tella, 2002) or because reduction of offspring predation due to coloniality was not sufficient to lead to increased clutch sizes (Beauchamp, 1999a). Anti-predation benefits might also affect other reproductive factors, such as number of broods produced (Beauchamp, 1999a). As such, the importance of anti-predation benefits as a significant driver for the initial evolution of coloniality remains open to debate, but it seems likely to contribute to colony maintenance.

2.4 Information for defence against brood parasites

Colonies represent an aggregated source of easily monitored potential hosts for both obligate heterospecific and opportunistic conspecific brood parasites (Brown & Lawes, 2007; Ležalová-Piálková, 2011). Both interspecific and intraspecific brood parasitism represent a significant cost to the host providing incubation and parental care to the offspring of the parasite (Brown & Bomberger Brown, 1989; Rothstein, 1990). Brood parasitism by conspecifics will benefit some members of the colony at the cost of others and individuals must rely on personal information to successfully

reject parasitic eggs (Gaston, De Forest & Noble, 1993; Ležalová-Piálková & Honza, 2008). However, when dealing with heterospecific brood parasites, animals can utilise social information for more effective protection (Campobello & Sealy, 2011b).

Studies have shown that, as with defence against predators, collective vigilance and copying the defensive strategies of more informed individuals can enhance the ability of individuals in larger colonies to detect and defend themselves against interspecific brood parasites (Campobello & Sealy, 2011b; Rands, 2012; Strausberger, 2001). While studies have shown that animals nesting in colonies suffer less from brood parasitism than solitary nesters (Clotfelter & Yasukawa, 1999), the effects of larger colonies have been mixed. In some cases larger colonies have been found to suffer less than smaller colonies (Brown & Lawes, 2007; Lawes & Kirkman, 1996; Lindholm, 1999; Strausberger, 2001), while other studies found that colony size had no effect above a certain threshold (Barber & Martin, 1997; Brown & Bomberger Brown, 1989; Ferguson, 1994). These studies suggest that defence against interspecific brood parasitism may have been a more important advantage during the initial evolution of coloniality. However as colonies grow, they can begin to represent a conveniently concentrated source of hosts for brood parasites. Therefore there is a trade-off between defence benefits gained and the increased conspicuousness of larger colonies (Barber & Martin, 1997; Brown & Bomberger Brown, 1989).

The importance of brood parasitism towards the maintenance of a colony is therefore likely to depend upon the level of experience a host has with a particular parasite species (Campobello & Sealy, 2011a; Payne, 1977). In such cases, inexperienced individuals will gain a benefit from copying the defensive decisions of more experienced individuals breeding in a colony, relying on social information

where they lack personal information (Campobello & Sealy, 2011b; Davies & Welbergen, 2009; Rands, 2012).

2.5 Information for behavioural coordination

2.5.1 Synchronous breeding

Highly synchronous breeding schedules are common in many colonial species, particularly birds (Darling, 1938; Hatchwell, 1991). Large numbers of breeders and young that are spatially clumped increase the effectiveness of anti-predation strategies, but this is most effective when they are also clumped in time (Darling, 1938; Ims, 1990; Nisbet, 1975). There is evidence that synchronous breeding cycles may be maintained by the ability to acquire information about conspecific's reproductive status via social cues (Hailman, 1964; Wilhelm & Storey, 2002). Breeding colonies provide easy access to such social information and it might therefore be expected that animals in breeding colonies would exhibit a higher degree of synchronicity than solitary breeders. Likewise we might also expect larger colonies to display higher breeding synchronicity (Darling, 1938; Jovani & Grimm, 2008). A comparison of colonially nesting brown-hooded gulls *Chroicocephalus maculipennis* with those breeding solitarily showed increased synchronicity in the birds breeding in colonies (Burger, 1974). However a study of breeding synchrony in fieldfares found no significant difference between different sized colonies (Wiklund, 1984). Several species show greater levels of synchronicity when social stimuli are increased, as might be found in larger colonies (Setiawan *et al.*, 2007; Waas, Colgan & Boag, 2005). A study of the common guillemot *Uria aalge* suggested strong stabilising selection favours the maintenance of synchronous breeding in colonies (Reed *et al.*, 2006). It seems likely that the easy synchronisation of breeding

behaviour is an important advantage of colonial breeding (Gochfeld, 1980; Wittenberger & Hunt Jr, 1985).

2.5.2 Synchronous migration departures

Migratory birds breeding in colonies can also share information in order to synchronise migration departures (Helm, Piersma & van der Jeugd, 2006). Synchronising departures can provide group anti-predation advantages (Leyrer, Pruiksma & Piersma, 2009) and can also allow the formation of structured flocks which can aid in navigation and reduce flight costs (Cutts & Speakman, 1994; Piersma, Zwarts & Bruggemann, 1990; Simons, 2004; Weimerskirch *et al.*, 2001). As with other anti-predation benefits, an initial aggregation must occur for this information to be available, which the potential advantages of synchronous departures cannot cause. As such these behaviours are more likely secondary benefits of colonial breeding rather than a cause.

2.6 Information for breeding habitat selection

Breeding habitat quality can vary enormously in time and space, and can have significant fitness implications. The decision of where to breed is therefore under strong selection pressure. While animals may draw on personal information from previous breeding experiences while choosing, they can also utilise social cues from conspecifics (Danchin, Boulinier & Massot, 1998a; Danchin *et al.*, 2004). Boulinier *et al* (1996) found that in colonial nesting black-legged kittiwakes *Rissa tridactyla*, prospecting increased until the peak of fledging, when the greatest amount of social information on reproductive success was available. Boulinier and Danchin (1997) explained colony choice based upon social cues using two theoretical models. The first examined recruitment to a colony by comparing two strategies: (1)

utilising conspecifics to prospect for patches and (2) random patch selection. The model predicted that prospecting should occur mostly in long-lived species, where patches are predictable but scarce (Boulinier & Danchin, 1997). The second model looked at colony fidelity and dispersal by comparing breeding decisions based solely on own success and those based on patch success. The second strategy meant that individuals take into account the success of conspecific neighbours, regardless of their own breeding success (Boulinier & Danchin, 1997). This could be important if a patch was high quality, but a random event caused an individual's reproductive attempt to fail. The second strategy was found to be the most efficient when the environment was patchy but predictable, as is the case with many colonial species (Boulinier & Danchin, 1997). Support for these theoretical models was demonstrated empirically by manipulating kittiwake clutches (Boulinier, McCoy et al. 2008). Birds whose clutches failed were more likely to return to the same breeding habitat the following year if their neighbours were successful, but when all clutches in the sub-colony failed, kittiwakes moved in a high proportion to a different patch the following year (Boulinier *et al.*, 2008).

The theoretical models of Boulinier and Danchin (1997) were expanded upon by Doligez et al (2003) to consider frequency and density dependent interactions between individuals. As in the previous models, assessing the breeding success of conspecifics was the best strategy in more predictable patches. However, the conspecific-attraction strategy (where patches are chosen based on the presence of conspecifics in the previous years) always persisted, even though theoretically it is one of the least efficient strategies. This is may be due to individuals using this strategy parasitizing information from those utilising other strategies (Doligez *et al.*, 2003). Alternatively, aggregations caused by conspecific-attraction might facilitate

more effective monitoring of conspecific reproductive success (Shields *et al.*, 1988; Stamps, 1988).

Coloniality could potentially evolve as a by-product of habitat copying caused by such information use (Fig. 2.1, Boulinier *et al.*, 2008; Danchin *et al.*, 1998a; Doligez, Danchin & Clobert, 2002; Doligez *et al.*, 2004a; Doligez, Pärt & Danchin, 2004b). In areas fulfilling the criteria described (patchy habitats with a high predictability) using information about conspecific breeding success will naturally lead to an aggregation of individuals who make similar decisions.

2.7 Information for Sexual Selection

It has been suggested that coloniality can increase the likelihood of encounters with potential partners for reproduction and the attraction between partners due to increased conspicuousness (Draulans, 1988). Colonial species often exhibit more intense visual signalling, over shorter periods than solitary breeding species. Visual signals are more effective in colonies due to more efficient information transfer, requiring less time spent displaying before encountering a suitable partner. However, the level of competition will also be higher, requiring more elaborate displays than solitary breeding systems (Draulans, 1988). Draulans (1988) first pointed out the similarity between the system described and leks. Both have social information (evolved signals and inadvertent cues) freely available to females, reducing the time and energy required to sample and select males (Balmford, 1991; Wagner, 1992; Wagner, 1998). Females would therefore be attracted to a concentrated area of males displaying in a colony, just as in a lek (Wagner, 1992). A potential problem with this hypothesis is that many colonial species are socially monogamous, with both parents sharing the burden of parental care. Remaining

together in the same area that mate selection occurred in after breeding is quite dissimilar to how promiscuous lekking species behave (Lack, 1968). However, there is evidence that many socially monogamous species are pursuing a mixed mating strategy by attempting to gain extra pair copulations (EPCs), that is, they are genetically promiscuous (Gladstone, 1979; Wagner, 1992).

With such evidence it may be useful to discuss the different models for the formation of such “hidden leks”, and how they can act as sources of information. One such model is the “hotshot model” which suggests that subordinate males copy a dominant male’s choice of territory. This frees secondary males from the costly task of assessing and selecting a territory where female encounters will be high based simply on personal information (Beehler & Foster, 1988; Wagner, 1998). Another model that could be relevant in this context is the “female choice” model. In this case the model predicts that males cluster in response to a female preference for comparing males side by side, simply bypassing males displaying alone. Assessing males in an aggregation reduces the cost of visiting multiple territories to gain information on their quality. A lek environment will also produce inadvertent social information on the quality of males through the outcome of fights.

These hidden leks can cause clustering of male territories, producing an aggregation of male-defended territories, which may lead to colony formation when these display territories merge with the nesting territories (Fig. 2.1, Richard H, 1993; Wagner, 1992; Wagner *et al.*, 2000). It is thought that the mating system of the Razorbill *Alca torda* represents an intermediate stage in this process, having separate “mating arenas” a little aside from the main colony (Wagner, 1992). Evidence has also been found for hidden leks within colonies of Purple Martin *Progne subis*, with older males actively recruiting younger males to the colony in

order to gain extra matings in a lek like environment (Danchin, Wagner & Boulinier, 1998b; Morton, Forman & Braun, 1990). Coloniality might evolve as a byproduct of the aggregations caused by the use of social information from hidden leks.

2.8 Commodity Selection

Aggregation due to habitat copying and aggregation due to sexual selection both involve the transfer of social information between group members (information on the environment and information on potential partners respectively). In both cases, aggregation is merely a side effect of the using the same source of social information to make decisions. This can be generalised as aggregation being a by-product of commodity selection. Rather than animals aggregating due to the advantages eventually gained from breeding in a group; initial aggregations instead form as a by-product of animals making similar decisions (such as selecting a mate or where to breed), due to utilising the same sources of social information when making those decisions. This does not dismiss the idea that there are potential advantages to breeding in groups, merely that a direct advantage from breeding in close proximity is not required for a colony to initially form (Danchin & Wagner, 1997; Wagner *et al.*, 2000). If this is the case, attempting to correlate breeding success or survival rates with breeding density may be the wrong way to approach questions about the evolution of coloniality as such benefits would only take effect after the formation of the colony (Danchin & Wagner, 1997; Wagner *et al.*, 2000).

A question arising from commodity selection is: if the selection of breeding habitats and partners results in aggregation, why aren't there even more colonial species? Wagner, Danchin *et al.* (2000) answer this by pointing out that many colonial species feed on food which is patchily distributed, ephemeral and

uneconomic to defend. When it is economical to defend food, animals will hold large territories resulting in the separation of breeders, preventing aggregation. If true, this suggests that aggregation is actually the default state of animals and that rather than requiring strong selective pressures to form a colony, it may actually require strong selective pressures to prevent a colony forming due to the social information use (Ramsay, Otter & Ratcliffe, 1999; Wagner *et al.*, 2000). In these situations, the behavioural processes involved in commodity selection could explain the formation of breeding colonies and their spatiotemporal dynamics, although this will also depend on factors affecting environment variability and the evolution of dispersal rather than philopatry.

2.9 Foraging information

2.9.1 Information Centres

Another potential advantage of coloniality is increased food finding efficiency due to social information provided by conspecifics, the “Information Centre” hypothesis (ICH) (Ward & Zahavi, 1973a). The hypothesis posits that breeding colonies and communal roosts are advantageous because they can act as information centres where individuals actively advertise and share information about the location of food sources (Ward & Zahavi, 1973a).

According to the requirements of information centres, prey must be patchy and ephemeral, sufficiently abundant that there is little competition for food and last long enough that an individual can make at least one return trip. Colony members must be able to assess the success of a returning individual, allowing successful individuals to be followed to the food source. Differences in individual success must be due to chance or individual’s ability to locate prey, not because of differing

abilities to exploit food patches. Following must improve the foraging success of unsuccessful individuals (Ward & Zahavi, 1973a).

It has proved difficult to gather empirical evidence in support of information centres using these requirements (Buckley, 1997b; Davoren, Montevecchi & Anderson, 2003; Mariette & Griffith, 2012; Mock *et al.*, 1988). Many of the predictions made by the ICH are confounded by the difficulty of separating information sharing from local enhancement and recruitment centre (see below) effects (Bayer, 1982; Buckley, 1997b; Danchin & Wagner, 2001; Mock *et al.*, 1988; Richner & Heeb, 1995; Richner & Danchin, 2001). The hypothesis also drew criticism for apparently requiring a form of reciprocal altruism (or relatedness), with several studies questioning why a successful forager would return to a colony and actively share the information about food patches. Critics have pointed out that it is highly unlikely that colony systems meet the requirements for reciprocal altruism. Without making assumptions about relatedness or cooperation, the evolution of reciprocal altruism would require that returning to the colony would be of benefit to the leader and that the costs to the leader would be smaller than the benefits to the follower. In the absence of reciprocal altruism (or evolutionary incentives in colony mate welfare) the proposed system seems incredibly vulnerable to cheats. It has therefore been claimed that the hypothesis was unworkable without a form of group selection taking place (Danchin & Wagner, 2001; Mock *et al.*, 1988; Richner & Heeb, 1995; Richner & Danchin, 2001).

2.9.2 Recruitment centres

Richner and Heeb (1995) proposed an alternative hypothesis to the ICH. The “Recruitment Centre” Hypothesis (RCH) states that individuals gain a benefit from

feeding within a group, either because it increases their foraging efficiency or for group defence reasons (Richner & Heeb, 1995). In this case it is in an individual's best interest to return to the colony and recruit others to a discovered foraging patch. This was considered more viable than the ICH as there is a payoff for both the follower and the leader (Danchin & Wagner, 2001; Richner & Heeb, 1996; Richner & Danchin, 2001). However this hypothesis might seem to also require group selection in order to explain why birds don't simply wait at the colony to be recruited. Richner and Heeb (1995) suggested that it is likely that the decision is frequency dependant, given that a wait and follow strategy will become unprofitable as waiting times increase (Danchin & Wagner, 2001; Richner & Heeb, 1995).

2.9.3 Two strategy hypothesis

Another alternative is the "two strategy hypothesis" (TSH), which suggests that because dominance status in a group is often related to an animal's ability to find and exploit food, subordinate birds utilise colonies to identify and follow dominant individuals to food, a form of information parasitism. This is tolerated by dominant individuals because of the preferential access to food patches they gain and because of the increased protection they receive by occupying the central position in the colony. In this hypothesis, different individuals aggregate for different reasons. It is similar to the RCH in that it suggests that the recruiter gains grouping benefits. However unlike the RCH, TSH suggests the advantage is at the colony itself rather than at the foraging site (Weatherhead, 1983). Aside from the initial paper presented by Weatherhead (1983), empirical support for the TSH has been sparse. Several studies reject the hypothesis out of hand because it requires a static hierarchy of food finding, dominance and roost settling. Even studies testing for it have either been unable to distinguish it from the RCH (Kerth & Reckardt, 2003) or

have found no evidence for it (Alonso, Bautista & Alonso, 1997; Schreiber & Chovan, 1986).

2.9.4 Inadvertent information transfer

These additional hypotheses further confused matters, as several of their predictions and requirements overlapped with those of the ICH (Marzluff & Heinrich, 2001). This led to debate over studies that had previously appeared to support the ICH, highlighting the difficulty of separating the different explanations empirically (Danchin & Wagner, 2001; Marzluff & Heinrich, 2001; Mock, 2001; Richner & Danchin, 2001). One issue raised in these debates was the lack of attention given to the non-deliberate transfer of information. Few empirical studies have dealt with the idea that foraging information may also be shared inadvertently via inadvertent social information (Richner & Danchin, 2001). Lachman et al. (2000) discussed how the inability of animals to hide information could affect information sharing and animal aggregations. They demonstrated using a theoretical model that if information was non-excludable then it was more difficult for selfish cheaters to invade an information sharing system. Costs of gathering information decreased as the size of an aggregation increased and information became more freely available (Lachmann *et al.*, 2000).

Barta and Giraldeau (2001) also produced a theoretical model that assumed information is non-excludable, using a producer-scrounger game. In this model individuals utilise either one of two strategies. Producers actively search for food, while scroungers wait and follow successful foragers to feeding patches. The value of these two strategies differs depending on several factors, such as the duration a food patch lasts, the distance to the patch from the colony, the value of a food patch

and the number of producers and scroungers in the population. The value of each strategy is therefore frequency dependant, meaning that cheaters who never search for food themselves cannot totally invade a population and as long as there is an advantage to being the first to discover a food patch, such that some individuals will always utilise the searching strategy. The evolutionary stable strategy of the model predicts that only a few individuals will leave the colony to actively forage for food, with the rest of the colony waiting and following (Barta & Giraldeau, 2001).

This leads to some very specific predictions about the environmental conditions in which an information centre will operate, which raises the possibility that the criteria for detection of information centres used in previous empirical studies may have been ineffective. For example, high frequency of leading, which has been used as a criterion for the ICH in many studies, is predicted to only occur in exceedingly ephemeral food patches, explaining why it has so rarely been found (Barta & Giraldeau, 2001). Utilising the relative frequency of food searching flights compared to following flights would be a more effective way of attempting to falsify the ICH than simply examining the frequency of leading behaviour (Barta & Giraldeau, 2001). If, as in these models, information transfer in information centre is actually a mild form of information parasitism then there is no need for any form of reciprocal altruism for the ICH to operate (Barta & Giraldeau, 2001; Lachmann *et al.*, 2000). In breeding colonies, parents must return to the colony to feed their young making it extremely difficult for an individual to hide their foraging success. Foraging success can also be inadvertently transferred in several other ways such as chick begging behaviour, fatness or arrival time at the colony (Bijleveld *et al.*, 2010; Iacovides & Evans, 1998).

Similar models of local enhancement and RCH allow further predictions about the strategies that would be adopted in these systems. If local enhancement was the only system operating, the wait and follow strategy would be exceedingly rare as searching would be far more efficient due to searchers being able to be informed of others food discoveries. It is highly unlikely that such an efficient level of local enhancement would exist in nature as most species that utilise local enhancement range over a very large area.

In a recruitment centre, the decision of whether to wait to be recruited or to set out and search is also frequency dependant, with the theoretical model suggesting that significantly more individuals will adopt a wait and follow strategy than in an information centre (Barta & Giraldeau, 2001; Richner & Heeb, 1995). These predictions may allow future empirical studies to distinguish between the different systems by examining the ratio of animals searching and following. Racine *et al.* (2012) specifically tested these predictions in a colony of ring-billed gulls *Larus delawarensis*. Although there was significant potential for social information transfer at the colony, birds did not appear to use it, showing little evidence of following behaviour (Racine *et al.*, 2012). However, the authors noted that there is increasing evidence that information transfer might take place outside or on the periphery of colonies (Machovsky-Capuska *et al.*, 2014; Racine *et al.*, 2012; Weimerskirch *et al.*, 2010). The “compass rafts” formed by Guanay cormorants *Phalacrocorax bougainvillii* in close proximity to colonies are thought to provide information about the direction of foraging patches (Weimerskirch *et al.*, 2010). Australasian gannets *Morus serrator* also appear to utilise similar rafts to gain information about potential foraging areas (Machovsky-Capuska *et al.*, 2014). As many seabirds form such assemblages just outside colonies, the potential for inadvertent information transfer

on the edges of colonies should be taken into account in future studies (Racine *et al.*, 2012; Waggitt *et al.*, 2014).

2.9.5 Foraging information in colonial roosts

While empirical studies showing the ICH operating in breeding colonies have been scant, several studies have presented evidence of information centres in colonially roosting species (Kerth & Reckardt, 2003; Marzluff, Heinrich & Marzluff, 1996; Ratcliffe & ter Hofstede, 2005; Wright, Stone & Brown, 2003). A study of common raven *Corvus corax* roosts drawing this conclusion sparked debate and criticisms, with arguments focusing on the original predictions of the ICH, namely that information centres would be an ultimate explanation of the formation of colonies (Marzluff *et al.*, 1996; Richner & Danchin, 2001; Ward & Zahavi, 1973a). The apparent need for reciprocity in information centres and the vulnerability of the system to cheats was also debated, as was the difference between recruitment centres and information centres (Danchin & Wagner, 2001; Marzluff & Heinrich, 2001; Mock, 2001; Richner & Danchin, 2001). One of the conclusions drawn was that in order to provide convincing evidence of the ICH in colonial roosts, it would have to be demonstrated that information centres are viable without reciprocal altruism (Richner & Danchin, 2001). A theoretical model based on the winter roosting colonies of juvenile common ravens demonstrated the opportunity of sharing foraging information alone could lead to the evolution and maintenance of recruitment to food in certain scenarios (Dall, 2002). The ability for foraging information alone to lead to this result depends on factors such the costs of recruitment, the benefits of being the first to discover a food patch and the advantage

gained from foraging in a group. The study concludes that while it is possible for ravens to forage independently and recruit, purely based on the sharing of patch location information (ICH) it is highly likely that group foraging benefits (RCH) also play a large part in the behaviours observed in juvenile ravens (Dall, 2002).

Further empirical study of raven foraging strategies, utilising carcasses baited with colour-coded plastic beads, seemed to provide further evidence of roosting colonies acting as information centres (Wright *et al.*, 2003). While the study observed birds searching independently and recruiting to carcasses, smaller sub-colonies of juvenile birds were seen searching and foraging together as a consistent group (Dall & Wright, 2009b; Wright *et al.*, 2003). This “gang foraging” behaviour had been predicted by theoretical models of raven behaviour, where it had emerged as a viable alternative to individual searching and recruitment (Dall, 2002). This model was readapted to investigate the conditions which could give rise to such an alternative social foraging strategy (Dall & Wright, 2009b). Gang-foraging emerged when prey was moderately difficult to find. If food was too easily available, individuals foraged alone, while if food was too difficult to find individuals returned to foraging individually and recruiting. This concurs with the highly specific prey type requirements for an information centre to operate and avoid being invaded by alternative strategies.

We might expect information transfer in colonial roosts to function differently to breeding colonies, due to the more flexible structure of roosts. Unlike breeding colonies, which consist of fixed nests, an individual’s positions within a colonial roost might change from night to night. It has been suggested that patterns of roosting might be related to the positioning of foraging areas or the foraging preferences of experienced individuals (Wright *et al.*, 2003). In breeding colonies, nest locations

remain fixed throughout a breeding season, meaning that initial choice of position within the colony will significantly affect reproductive success (Barbosa *et al.*, 1997; Liljeström *et al.*, 2008). Other forms of information (such as conspecific reproductive success in previous years, as mentioned earlier) are more valuable in making this decision than conspecific foraging success or food patch location (Boulinier *et al.*, 2008). The structure of a breeding colony is therefore unlikely to be affected by information about foraging areas. In contrast, when arriving at a colonial roost naïve individuals can choose to roost near a knowledgeable individual following having been recruited, in the hope of accruing further information benefits (Wright *et al.*, 2003). If this is the case, enhanced foraging due to information benefits or recruitment benefits, might have a direct effect on the formation of colonial roosts.

2.9.6 Can enhanced food finding lead to colony formation?

The information centre hypothesis proposed that enhanced food finding was one of the main reasons for the evolution of colonial breeding (Ward & Zahavi, 1973a). All of the theoretical models mentioned make an assumption that an aggregation already existed, examining how the transfer of foraging information could maintain an aggregation. No studies have examined how transfer of foraging information could cause aggregations, which could then lead to the evolution of colonies. While a previous study by Horner (Horn, 1968) suggested that enhanced food finding may be a reason for aggregation, this study focuses primarily on the central placement of colonies within a patchy mosaic of food sources (Horn, 1968). Sharing of foraging information is seen as a possible secondary benefit after aggregation of nests already occurred. Originally seabirds were presented as potential evidence that enhanced food finding can lead to aggregation and coloniality. The fact that 98% of seabirds breed colonially seems to exemplify the

idea that, when faced with an unpredictable environment where feeding territories cannot be held, individuals will evolve to become colonial in order to best exploit food sources, possibly by the sharing of foraging information (Wittenberger & Hunt Jr, 1985). Indeed there is direct evidence that foraging seabirds make use of social information throughout foraging bouts (Votier *et al.*, 2013; Weimerskirch *et al.*, 2010) and colonial-specific home ranges of some seabirds may be enhanced by individual use of social information in the form of local enhancement and recruitment centres (Wakefield *et al.*, 2013a).

However a comparative study by Rolland *et al.* (1998) examining the evolution of coloniality cast doubt on food finding as a driver of aggregation and coloniality. While coloniality is ultimately highly correlated with marine environments and indefensible feeding patches, these environmental factors were not necessarily the cause of the evolution of coloniality (Rolland *et al.*, 1998). For example, there are several solitary species that do not defend feeding territories (such as carrion crows *Corvus corone* or flycatchers *Ficedula sp.*) and several colonial species that do (black headed heron *Ardea melanocephala* or the great egret *Casmerodius albus*). Colonial species likely went through intermediate stages where they lived colonially but still held feeding territories or lived solitarily but did not defend feeding territories (Fig 2.1). Analysis suggests that solitary species rarely evolved to occupy marine habitats and coloniality evolved significantly before species made such a transition. This may suggest that many species of colonially breeding seabirds were already colonial non-marine, non-territorial feeders before they moved to a marine environment. Terrestrial conditions favoured the loss of feeding territories, and the passage to marine life. Thus, coloniality may have pre-adapted marine species to allow them to successfully exploit a marine environment. This contradicts the idea of

the unpredictable nature of a marine environment driving the evolution of seabird coloniality (Rolland *et al.*, 1998). Additionally it is suggested that terrestrial environments might be just as unpredictable as marine environments (Rolland *et al.*, 1998). The colonial *Hirundinidae* and *Apodidae* species included in the analysis feed on swarms of insects which are just as ephemeral in space and time as marine prey species. Recent studies have also shown that the behaviour of many marine species is frequently very consistent, suggesting that the marine environment is more predictable than previously thought (Cama *et al.*, 2012; Grecian *et al.*, 2012; Ramos *et al.*, 2013).

2.10 Future Study

While the evolutionary origins and benefits of coloniality are still unclear, recent theoretical, empirical and evolutionary studies have shed light on what can cause and maintain breeding colonies. Information use pervades all aspects of colonial living and understanding the mechanisms by which it assists decision-making is vital for future study. It is important to distinguish between decisions that are assisted by the easy availability of social information in colonies and decisions that can cause aggregation as a by-product (Danchin *et al.*, 2008). Several studies have shown how colonies might form as a side effect of animals making similar decisions due to using the same sources of social information (Danchin & Wagner, 1997; Wagner *et al.*, 2000). Others demonstrate how the easy availability of social information leads to improved decision making, helping maintain breeding colonies in the face of the potential disadvantages associated with large static aggregations (Arroyo *et al.*, 2001; Boulinier *et al.*, 2008; Doligez *et al.*, 2004a; Hernández-Matías, Jover & Ruiz, 2003). It will be necessary to disentangle these advantages and assess how they and their interactions contribute to the maintenance of colonies for

future studies of coloniality. Better understanding of how animals use inadvertent social information will require the studying of the decisions of individuals, both in and outside the colony (Barta & Giraldeau, 2001). While in the past this has proved challenging (Brown & Brown, 1987) developments in bio-logging technology are making the monitoring of an animal's behaviour easier, even when animals are out of sight of the colony (Ponchon *et al.*, 2013; Robson *et al.*, 2004; Thiebault *et al.*, 2014; Votier *et al.*, 2013; Wilson *et al.*, 2007). One of the main areas of interest benefiting from improvements in technology is studying the ability of individuals to monitor conspecific behaviour in order to make decisions. For example, further study into the mechanisms by which failed breeders assess conspecific breeding success could provide information on the mechanisms and cues behind the formation of breeding colonies (Ponchon *et al.*, 2013; Votier *et al.*, 2011). Similarly the combination of GPS and camera technology allows the gathering of evidence of following to food patches or other modifications to foraging behaviour due to social information (Thiebault *et al.*, 2014; Votier *et al.*, 2013).

Future studies might also examine animals' awareness of colony size or neighbour density and how this affects their behaviour. However, further thought should be given to which colony sizes to compare, and how these colony sizes are measured. Comparing large colonies with small colonies may be useful in establishing the benefits of existing aggregations, but will tell us little about the formation of these aggregations (Danchin *et al.*, 1998b). In an ideal world we would study a species at every stage of the transition to coloniality (Fig. 2.1). Animals which breed both colonially and solitarily are useful for examining how the transition to coloniality might affect individuals, but species engaging in both strategies are rare (Mariette & Griffith, 2012; Neff *et al.*, 2004; Sasvári & Hegyi, 1994). Measuring

colony size simply by number of pairs or nests might also be inappropriate. Different colonies can display extremely varied spatial structures, and different areas can face different selection pressures (Aebischer & Coulson, 1990; Brunton, 1997; Coulson, 1968; Veen, 1977). This should be taken into consideration in empirical studies, especially when examining social information use, where the structure of the colony and density of neighbours will have significant effects on the information available (Jovani & Tella, 2007).

Ultimately, some form of “common currency” is required to best assess the various benefits of coloniality (Danchin & Wagner, 1997; McNamara & Houston, 1986). The metrics that have traditionally been used in cost-benefit approaches, such as survival rate or clutch sizes, have proved to be unsuitable for assessing the effects of the wide range of potential advantages that a colony can provide (Danchin & Wagner, 1997). Measuring the conspecific cues used by animals to assess safety, breeding sites, mates and food when making decisions about habitat may lead to such a common currency, which would be correlated with the fitness costs and benefits of coloniality (Danchin & Wagner, 1997; Piersma *et al.*, 1990). For breeding colonies, one possibility is reproductive success, which may provide information about the quality of a breeding patch to both animals and researchers (Brown, 1988; Danchin & Wagner, 1997; Danchin *et al.*, 1998a). Reproductive success naturally combines several fitness components making it an extremely useful metric to measure the advantages and disadvantages of coloniality and their effects on individuals within the colony (Danchin & Wagner, 1997; Danchin *et al.*, 1998a). Reduced predation and parasitism, enhanced food finding and increased synchronicity are all likely to increase reproductive success (Danchin & Wagner, 1997). Reproductive success can also be used as a cue by prospecting conspecifics,

leading them to make similar decisions about where to breed without having to spend time assessing the environment or all the advantages a colony might bring. As such it is a useful measure for both animals and empirical researchers studying the evolution of coloniality. However there remains the difficulty of disentangling the use of social information from the use of environmental cues which might be correlated with reproductive success (Doligez *et al.*, 2002). Several studies have avoided this by artificially manipulating breeding success (Aparicio, Bonal & Muñoz, 2007; Boulinier *et al.*, 2008; Doligez *et al.*, 2002). Additionally it is highly unlikely that prospecting animals will rely on the mean reproductive success at a patch since quality might still be highly variable (Aparicio *et al.*, 2007; Kosciuch & Langerhans, 2004). Kosciuch and Langerhans (2004) suggest that animals might also take the variance of reproductive success into account when selecting a colony to settle in, though a study of Lesser Kestrels *Falco naumanni* found no evidence of this (Aparicio *et al.*, 2007). Variance in reproductive success may however be more important for other species such as seabirds and future studies should ensure that all potential cues of reproductive success are taken into account. Whatever common currency is used, information clearly plays an integral part in the formation and maintenance of colonies. The study of social information and its effects on the decision making of animals will provide great insight into the mechanisms behind colonial living.

2.11 Conclusions

1. Information use is an integral part of colonial living. Colonies act as sources of social information, allowing animals to make more informed decisions about reacting to predators, migration, habitat choice mate choice and foraging.
2. Easy availability of social information is one of the main advantages, allowing the maintenance of the large aggregations of animals that colonies represent.
3. The aggregation of animals into colonies might be a side-effect of individuals making similar decisions based on social information.
4. Greater knowledge of how animals make the decisions that lead to the emergence and subsequent maintenance of colonies will inform further research into how colonial breeding evolved in the first place.

3. GPS tracking reveals European shags *Phalacrocorax aristotelis* from neighbouring colonies have shared foraging grounds



3.1 Abstract

Developments in tracking technologies have enhanced our understanding of the behaviours of many seabird species. However, few studies have examined the social aspects of seabird foraging behaviour, despite the effect this might have on the distribution of foraging areas and the differences that might arise between colonies. Here we use bird-borne GPS to study the foraging behaviour and habitat use of breeding shags from three breeding colonies in the Isles of Scilly. Thirteen breeding shags from three colonies (six at two colonies, and a single bird from another) were tracked in the Isles of Scilly between 2010 and 2012 and related this to observed data on conspecific foraging aggregations (2013 - 2014) and bathymetry. Tracked shags had short foraging ranges (1.74 ± 1.6 km) mostly travelling to shallow waters between the islands. Observations in these same waters revealed large foraging groups of shags between that were consistent in time and space. There were no clear differences in foraging distribution among the colonies – birds shared similar foraging grounds. Differences in bathymetry were not correlated with foraging behaviour. Our results reveal that shags foraged in shallow waters in large conspecific aggregations, which lead to birds from different colonies having shared foraging grounds. These results differ from previous studies which found segregation of foraging areas of birds from neighbouring colonies.

3.2 Introduction

Recently there have been great advances in the use of technology for tracking animals, particularly seabirds. Devices are increasingly sophisticated, lighter and cheaper, offering new insight into the distribution and behaviour of previously understudied species (Burger & Shaffer, 2008).

Seabirds feed on prey that is patchy and heterogeneous (Hunt, 1990; Weimerskirch, 2007), though highly predictable at certain scales (Scales *et al.*, 2014; Weimerskirch, 2007). This strongly shapes their foraging behaviour and life history characteristics (Dobson & Jouventin, 2007). Tracking research reveals some species are highly site faithful to features such as ocean-fronts (Scales *et al.*, 2014) while others that feed on unpredictable prey display no clear site fidelity (Sydeman *et al.*, 2001; Weimerskirch *et al.*, 2005; Weimerskirch, 2007). Locating suitable foraging sites may be aided by sensory or learned processes, but information obtained by observing the behaviour of others (social information) may also play an important role (Dall *et al.*, 2005a). Social information can either be gathered within and around the colony (Machovsky-Capuska *et al.*, 2014; Waggitt *et al.*, 2014; Weimerskirch *et al.*, 2010), or at sea (Thiebault *et al.*, 2014). Birds can utilise a variety of cues to find prey, such as a returning conspecifics' direction of travel (Thiebault *et al.*, 2014; Weimerskirch *et al.*, 2010), the feeding behaviour of conspecifics and heterospecifics (local enhancement, Davoren *et al.*, 2003; Goyert, Manne & Veit, 2014; Silverman, Veit & Nevitt, 2004), the presence of conspecifics (Beauchamp, Belisle & Giraldeau, 1997; Porter & Sealy, 1982) or even anthropogenic activity (Votier *et al.*, 2013). The information centre hypothesis suggests that transfer of social information about prey at colonies is one of the main advantages of coloniality (Bijleveld *et al.*, 2010; Ward & Zahavi, 1973b). An important requirement of this hypothesis is that information about food location must be valuable enough that using information gained from conspecifics at the colony will result in more efficient foraging (Barta & Giraldeau, 2001; Ward & Zahavi, 1973b), which will depend on the difficulty of finding prey (Racine *et al.*, 2012). Accessing social information at colonies might be more valuable if prey is patchy and ephemeral (Barta & Giraldeau, 2001), while birds

feeding on predictable prey can rely on a combination of memory and simple conspecific attraction to find prey patches (Davoren *et al.*, 2003). Studies of seabirds from multiple colonies have also shown that social information use might lead to colony-specific foraging ranges due to learning prey distribution from conspecifics (Wakefield *et al.*, 2013b).

The majority of seabird tracking studies have been carried out on medium-ranging (70-1200 km), pelagic birds (Paiva *et al.*, 2010; Votier *et al.*, 2010; Votier *et al.*, 2013; Weimerskirch *et al.*, 2002) with comparatively few studies of short ranging, coastal seabirds (~20 km, but see: Cook *et al.*, 2012; Kotzerka, Hatch & Garthe, 2011; McLeay *et al.*, 2010). This disparity has implications for our understanding of a wider range of applied and theoretical questions (Wakefield *et al.*, 2013b). Shags and cormorants (Family: *Phalacrocoracidae*) are colonial breeding, inshore pursuit diving seabirds consisting of around 40 species that breed at high latitudes in both hemispheres as well as in tropical waters (Nelson, 2005). The European shag *Phalacrocorax aristotelis* (hereafter 'shag') breeds around the Atlantic and Mediterranean coasts of Europe and typically forages in sandy, rocky areas at depths of up to 60 metres, mainly on small fish, supplemented by crustaceans (Nelson, 2005). Shags can also engage in group foraging behaviour, forming large rafts, often consisting of long belts of several hundred individuals moving and diving together (Nelson, 2005). While in these assemblages birds will regularly "leap frog" each other, with birds from the back flying to the front of the group where they immediately begin diving, which may provide foraging benefits (Anker-Nilssen, 2009). Similar behaviours can be found in several other *Phalacrocorax* species around the world (Nelson, 2005). Though foraging rafts have been observed in numerous locations, they appear to form most frequently in proximity to large

colonies (Anker-Nilssen, 2009; Velando & Munilla, 2011). Because of their preference for coastal habitat and collective behaviour, shags may be especially prone to disturbance, for instance because of the impact of marine renewable energy installations (Furness, Wade & Masden, 2013; Grecian *et al.*, 2010). Despite this, there are only a few published tracking studies of this species (but see Soanes *et al.* (2014) and Bogdanova *et al.* (2014)), and none that has specifically investigated the role of group foraging or compared distributions among multiple colonies.

The current study focuses on shags on the Isles of Scilly (49.9361° N, 6.3228° W). This archipelago consists of five inhabited islands and roughly 300 rocks and uninhabited islands. The islands are a Special Protection Area under EU law, in part because of the seabird assemblage of international importance (Heaney *et al.*, 2008). Approximately 20,000 seabirds, of 13 different species breed within the islands, including ~1300 breeding pairs of shags (Heaney *et al.*, 2008). Here we describe the foraging behaviour of shags in the Isles of Scilly using a combination of high-resolution GPS tracking of breeders from three colonies in tandem with observations of group foragers of unknown status. We examine how foraging behaviour is affected by bathymetry (depth and slope), how foraging varies between birds from different colonies and also link tracked birds with the location of foraging rafts.

3.3 Methods

3.3.1 Fieldwork

Shags were caught (with permission from the Isles of Scilly Wildlife Trust) while on the nest during April - June 2010 - 2012, at the three largest breeding colonies within the Isles of Scilly archipelago; Annet (96 pairs; Heaney, V. pers.

comm.), Samson (35 breeding pairs; Heaney *et al.* (2008)) and The Ganninicks (62 pairs; Heaney, V. pers. comm.). After capture, shags were colour-ringed (to enable resighting) and equipped with a GPS logger (iGOTu GT-120, Mobile Technology), under licence from the British Trust for Ornithology. Loggers were modified by removing their original casing and sealing them in heat shrinking plastic, in order to improve water resistance and reduce weight. Tags were attached to the back feathers of birds using Tesa© tape (#4651, Tesa Tape, Inc.) so that unrecovered, tags would fall off. GPS device and attachment materials weighed 17g in total, <1% of typical shag body weight. After device activation, position was logged at 100-second intervals, giving an approximate recording time of 3 days (Table 3.1), after which the bird was recaptured at the nest and the tag recovered so as to download the data.

3.3.2 Rafting observations

In order to generate a dataset of shag rafting behaviour with which to compare our GPS tracking, we conducted systematic observations of rafting birds around the archipelago. Observations were made from the islands of St Marys and St. Agnes during 2013 and 2014. Data were collected throughout an entire lunar tidal cycle including spring and neap tides. The circumferences of the two islands were divided into patrol sites of roughly equal length, six on St Marys and three on St Agnes. Each of these patrol sites contained six observation points. Patrols lasted two hours in total, with observers spending 15 minutes at each observation point. Three patrols were carried out daily between 3/5/13 - 8/7/13 and 1/5/14 - 1/6/14, from 8:00 - 10:00, 11:00 - 13:00 and from 14:00 - 16:00. For each time of day, we recorded data at tidal ebb and flood and at three different speeds of tidal flow, based on the rule of twelfths (a method for estimating tidal flow, assuming that during a 6-hour

tidal range the tide rises or falls in twelfths of its range in the pattern: 1, 2, 3, 3, 2, 1). The patrol sites visited each day were pseudo-randomly selected based on what combinations of site, tidal state and time of day had previously been sampled. When a raft was spotted the exact observer coordinates were recorded using a GPS logger (eTrex Summit® HC, Garmin Ltd.). Movements of rafts were recorded until it dispersed or was lost from sight. During observations, the raft was constantly filmed using a video camera (Sony Handycam HDR-CX190E, Tokyo, Japan). Bearings of the raft relative to magnetic north were taken every five minutes using a compass or more frequently if shags flew from one location to another. In this case the bearing at the beginning and end of the flight event were recorded. Raft size was also recorded every five minutes, unless the raft underwent a sudden change in size. If the raft split into multiple smaller rafts, we continued tracking the largest.

Bearings were plotted as lines from the observation point using ArcGIS (ESRI, 2012). In order to estimate distance along the bearing we used a 3d representation of the Scillies (Terrain data acquired from Ordnance Survey Land-Form PROFILE dtm dataset (2009)), detailed charts acquired from SeaZone Solutions HydroSpatial One dataset (2015) using ArcVIEW which we matched with the video footage, allowing us to plot the location of rafts within the islands. To quantify where in the islands rafts regularly form, these positions weighted by the number of individuals within a raft were used to calculate a utilisation distribution (UD) kernel estimation (Worton, 1989) using the R package, adehabitatHR (Calenge, 2006), in R 3.1.1 (R Core Team, 2014).

3.3.3 Analysis of tracking data

Based on bird-derived GPS fixes, First Passage Time analysis (FPT) was used to identify at-sea foraging locations (Fauchald & Tveraa, 2003). First Passage Time is the time taken by an animal to cross a circle of a given radius. Peaks of variance in the log transformed FPT are used to identify the presence of area restricted search behaviour (ARS) (Fauchald & Tveraa, 2003). ARS is characterised by decreases in speed and increases in turning, assumed to represent an increase in foraging effort in order to exploit areas of high prey density (Weimerskirch, Wilson & Lys, 1997). The radii at which the peak in variance occurs represent the ARS scales at which this increase in search effort occurs. By recalculating FPT at this spatial scale and inspecting a plot of FPT over the course of a foraging trip, the spatial locations where ARS takes place can be identified (Fauchald & Tveraa, 2003).

GPS datasets were split into multiple sections by determining when a bird returned to the nest or perched on a rock using an R script. Fixes in these areas were excluded from further analysis in order to avoid spurious detection of ARS. FPT was calculated at intervals of 100 seconds (with interpolated points where tracks were irregular due to missing fixes etc.) for each individual trip, using the R package, *adehabitatLT* (Calenge, 2006), in R 3.1.1 (R Core Team, 2014). Plots of the variance of log transformed FPT against a series of radii from 1m to 5000m were used to identify peaks of variance for each trip (Fig. A3.1). The radii at which these peaks occurred were used to calculate a mean ARS scale for each individual (Table A3.1). FPT profiles at the appropriate spatial scale for the trips of each individual were split into homogenous sections of ARS or commuting flight, using techniques based on Lavielle segmentation (Lavielle, 1999; Lavielle, 2005).

Utilization distribution (UD) kernel estimations (Worton, 1989) with a grid of $600 \times 600 \times 60 \text{ m}^2$ cells and ad-hoc calculation of smoothing parameters (selected bandwidth = 575 m) were generated from the ARS regions using R package, `adehabitatHR` (Calenge, 2006) to quantify foraging areas. Utilisation distributions were calculated in two ways: (i) by colony (Fig. 3.2), (ii) by foraging trip (Fig. 3.2). The between-colony and between-individual overlap of ARS zones were calculated using 50% kernels. All maps were plotted using ArcGIS (ESRI, 2012).

In order to examine the bathymetric conditions of shag foraging areas, we extracted the top 20% (which represented the key foraging area of a trip) of utilisation distribution kernels of ARS zones to create a hotspot polygon (Fig. A3.2). For each hotspot, we also calculated the sum of FPT, area, distance from colony, median bathymetry and median slope of bathymetry. Median values were used to minimize the effect of differences in ARS scales and reduce the influence of extreme values. We also investigated which foraging hotspots fell into the top 95% of an utilisation distribution kernel generated from the observed positions of rafts. Bathymetric data was acquired from SeaZone Solutions Gridded Bathymetry dataset (2015).

3.3.4 Statistical analyses

In order to explain variation in the location of foraging hotspots (based on the location of ARS behaviour) we used linear mixed effects models including an exponential spatial autocorrelation structure. The sum of FPT in a hotspot divided by the distance travelled in a hotspot (which we used as a measure of foraging effort) was fitted as the response variable. Predictor variables were: year, home colony, distance of foraging hotspot from home colony (km), median bathymetry of hotspot

(m below lowest astronomical tide), medium slope of bathymetry in hotspot (degrees), and whether that foraging hotspot was within an area where rafts frequently form (0/1). Due to birds having multiple trips and some multiple hotspots, Bird ID and trip ID were fitted as random effects.

Measures of bathymetry, bathymetric slope and distance from colony were grand mean centred by subtracting the mean from each datapoint (Hofmann & Gavin, 1998). This was done so as to make model estimates of these effects easier to interpret. Response variables were log transformed in order to satisfy normality. All models were run using the R package nlme (Pinheiro *et al.*, 2014). The most parsimonious models were selected using Akaike's second order Information Criterion (AICc, Burnham & Anderson, 2002) using the R packages MuMin (Bartoń, 2014). For competing models with a $\Delta\text{AICc} < 2$, we carried out model averaging and selected the variables whose confidence intervals did not cross zero.

3.4 Results

3.4.1 Rafting observation results

During May to July 2013-14 95 rafts were recorded in total, with a maximum size of approximately 500 birds and a mean size of 177 birds. Rafts only formed within the main channels, with no rafts observed on the eastern side of the islands or outside of the shallow waters surrounding the Scillies (Fig. 3.3). Rafts were particularly concentrated in the shallows in the north of the islands and near Annet. Large rafts consistently formed in these areas throughout the periods of study, during both years, and were consistent with anecdotal observations from previous years.

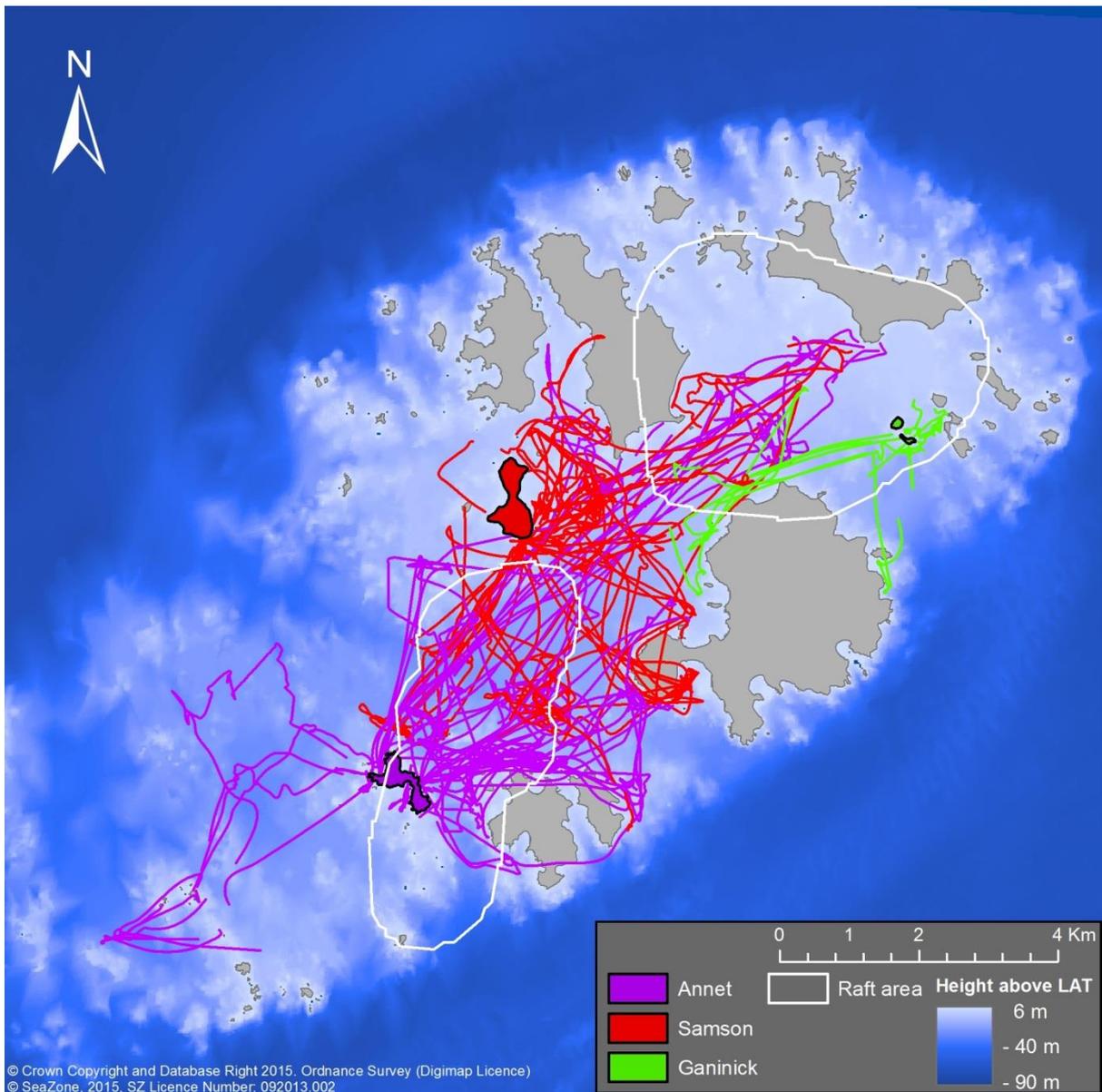


Figure 3.1: Foraging behaviour of breeding European shags on the Isles of Scilly, UK. GPS tracks of foraging trips of all birds tracked from three colonies in comparison to bathymetry and areas where rafts frequently form. Raft area contour represents the 75% contour of Utilization Distribution (UD) from Kernel analysis on the location of rafts weighted by the number of individuals in rafts (though this data is not contemporary to the tracking data). LAT=Lowest astronomical tide

3.4.2 Tracking results

Three GPS loggers were recovered in 2010, seven in 2011 and three in 2012 resulting in six datasets for Annet, six for Samson and one for The Ganinicks (Table 3.1). As only a single logger was recovered on the Ganinicks, these data area excluded from statistical comparisons between colonies. In total the loggers recorded 38 days of behaviour. ARS was found to occur on 118 (72%) of the 163 recorded trips. Shags mostly restricted their inferred foraging to channels between islands, rarely foraging outside the main sound (Fig. 3.3). Birds foraged over a wide variety of spatial scales with some covering areas as large as 6.9 km while others only ranged over an area of 0.18 km (Table 3.1), most zones of ARS were within a short distance of a bird's home colony (Table 3.1; Fig. 3.3). Birds from Annet were more likely to travel further and over larger areas and were the only tracked birds to leave the main sound (Fig. 3.1, Table 3.1). Shags spent a fairly small amount of time at sea: < 20% (Table 3.1). The median bathymetry and bathymetric slope of UD's suggested birds mainly forage in flat and shallow areas (Table 3.1; Fig. 3.3).

Table 3.1: Descriptive statistics of European shag foraging behaviour on the Isles of the Scilly. LAT = lowest astronomical tide. Foraging hotspots represent the top 20% of the kernel UD calculated from identified areas of ARS for each colony and individual

Colony/Bird ID	Year	Tracking time (days)	% Time spent at sea	Number of foraging trips	% Of foraging hotspots in rafting area	Mean distance of hotspots to colony (km)	Mean area of hotspots (m ²)	Average of median bathymetry of hotspots (m above LAT)	Average of Median bathymetric slope of hotspots (degrees)
ANNET		18.3	13.55	55	74.55	2.08	16.59	-9.46	2.17
3	2010	3	17.54	8	87.5	3.99	22.47	-5.96	1.64
4	2011	3.3	14.57	9	100	1.15	3.35	-4.87	3.21
5	2011	3.6	12.64	9	11.11	2.35	6.87	-23.72	1.31
9	2011	3.4	18.21	11	81.82	0.95	10.83	-11.32	2.23
10	2011	1.6	18.82	5	80	4.4	10.64	-6.15	0.99
11	2012	3.5	21.72	13	84.62	1.66	33.48	-4.62	2.66
SAMSON		16.2	18.77	50	68	1.56	7.54	-5.24	0.98
1	2010	2.4	13.27	10	80	1.4	12.23	-2.16	0.55
2	2010	2.7	16.33	7	100	2.1	2.02	-17.73	1.42
6	2011	1.9	13.47	4	75	0.98	12.32	-2.05	0.3
7	2011	3	17.67	8	25	2.6	15.56	-4.32	1.32
8	2011	2.9	9.37	9	55.56	0.51	1.11	-0.03	0.78
13	2012	3.2	17.59	12	75	1.49	5.79	-2.9	1.07
GANINICK 12	2012	3.5	15.58	13	92.3	1.02	5.32	-2.12	2.06

The 50% utilisation distributions of birds from Annet and Samson showed some overlap, with 30% of the UD of Samson birds overlapping with that of Annet birds. Annet birds overlapped less with Samson birds, with a kernel overlap of 25% (Fig. 3.2). Investigation into the overlap of the 50% UD of individuals' showed that most individuals showed a higher degree of overlap with other individuals from their home colony (mean overlap: $20\% \pm 29\%$ SD) than those from other colonies (mean overlap: $10\% \pm 20\%$ SD). The UDs of birds from Annet were less likely to overlap with those of birds from other colonies (mean overlap: $4\% \pm 9\%$ SD) than Samson (mean overlap: $15\% \pm 26\%$ SD). Birds from both colonies spent a large amount of time foraging in areas where rafts were found to frequently form (Table 3.1; Fig. 3.1). Birds from Annet were found to forage slightly more in these areas (74.55%) than those from Samson (68%).

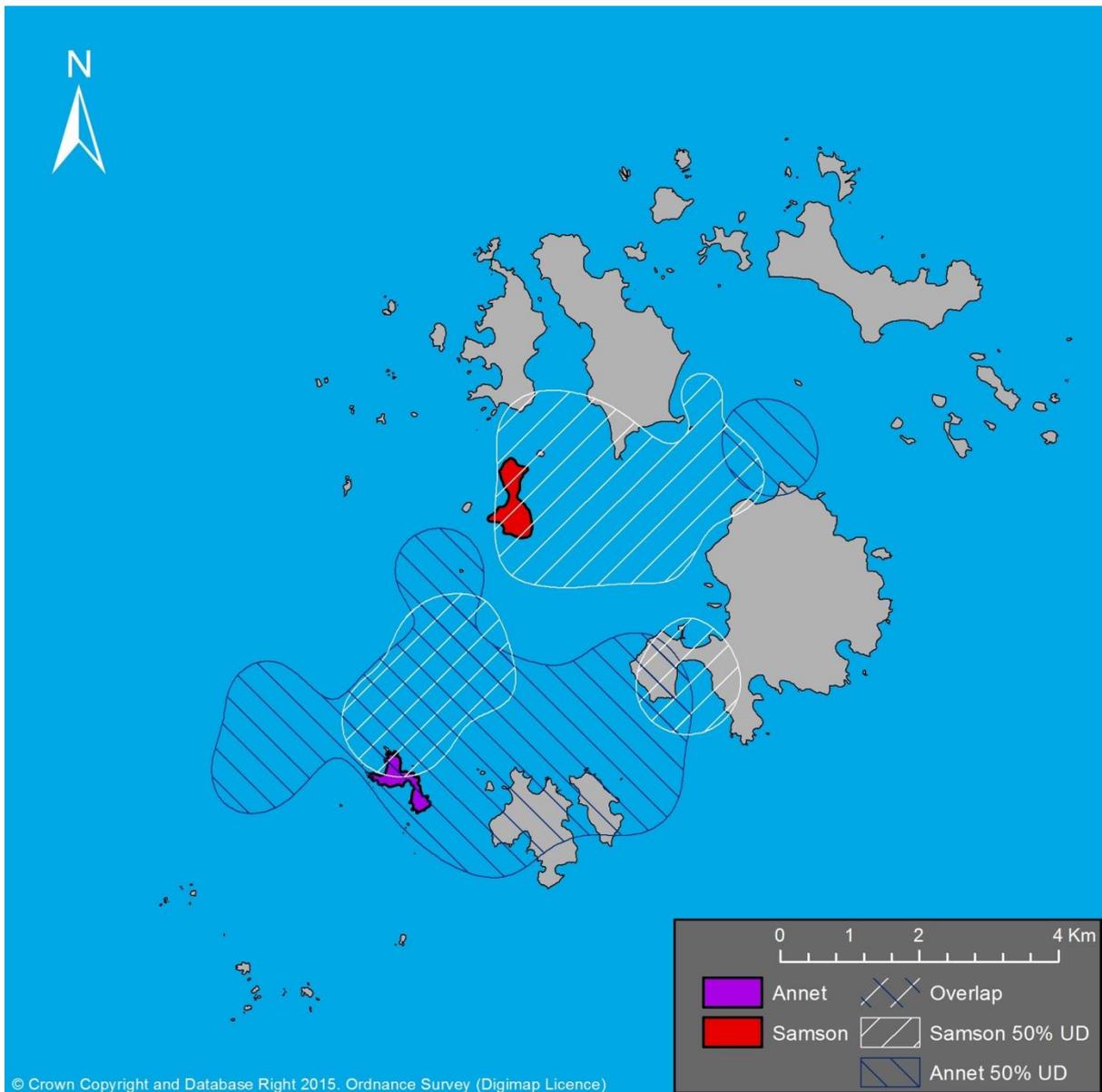


Fig 3.2: Kernel overlap between shags from the colonies of Annet and Samson. Kernel calculated from areas of identified Area Restricted Search.

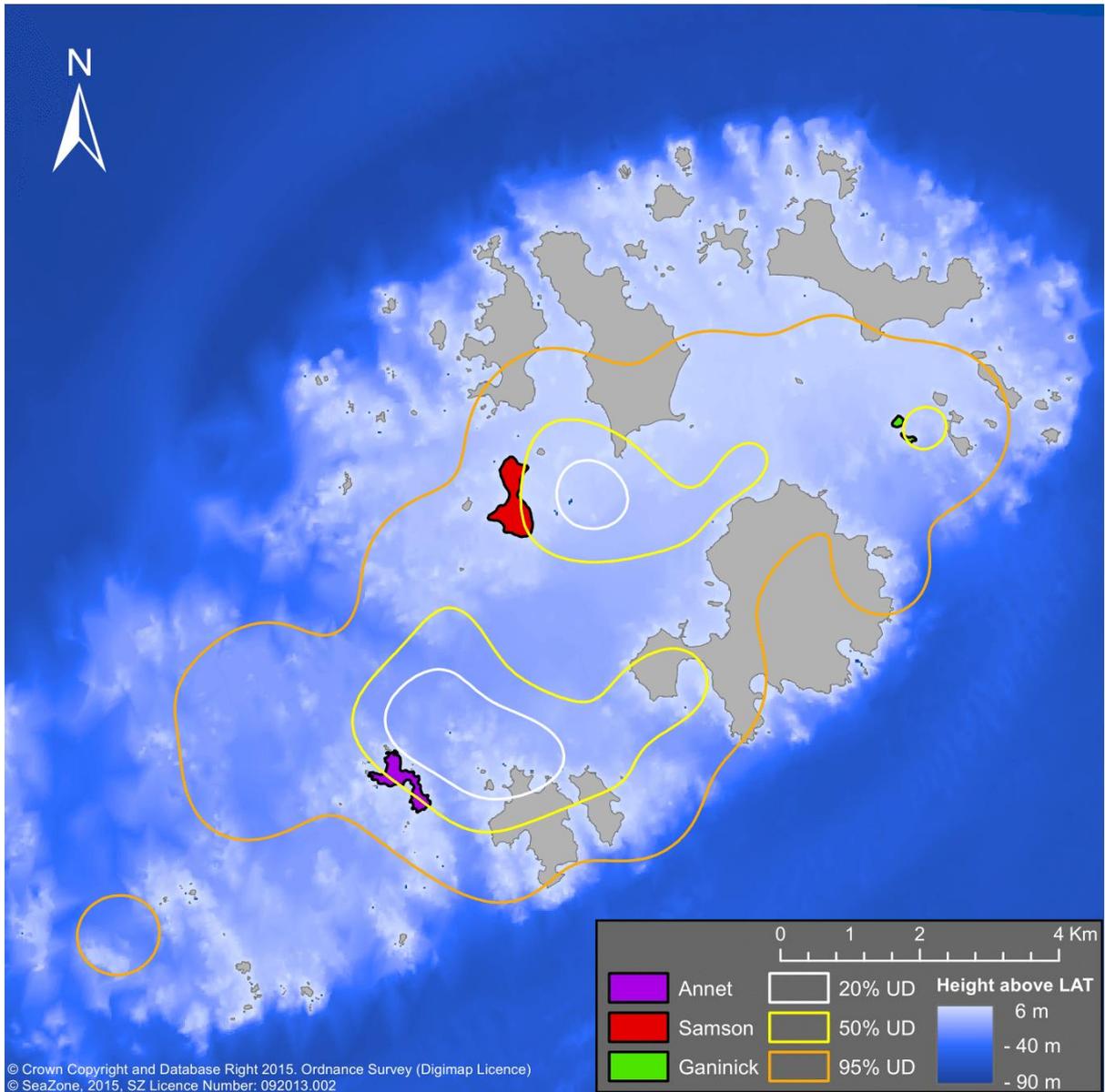


Figure 3.3: Map showing distribution of Area Restricted Search in European shags in comparison to bathymetry in the Isles of Scilly. Lines indicate 95, 50% and 20% contours of Utilization Distribution (UD) from Kernel analysis on the areas of ARS of all birds. LAT=Lowest astronomical tide

After carrying out model averaging no relationship was found between putative foraging effort in a hotspot and any environmental conditions (Table 3.2). Similarly, no significant change in foraging effort was found in rafting areas.

Table 3.2: Model averaged estimates of factors effecting foraging effort with 95% confidence intervals, based on the models within 2 Δ AICc of the top model.

Parameter	Weight	Estimate	2.5 % Confidence Interval	97.5 % Confidence Interval
Intercept		1.43	0.26	2.59
Home colony	0.81	1.00	-0.09	2.10
Within raft area	0.66	-0.79	-1.71	0.14

3.5 Discussion

This study gives new insight into the foraging behaviour of European Shags, highlighting the importance of inshore waters and that birds from neighbouring colonies foraged together in rafts. The implications of our findings for inshore foraging seabirds in general and Shags in particular are discussed below.

During the breeding season, shags on the Isles of Scilly foraged mostly in the shallow waters within the archipelago (Fig. 3.3), although one individual foraged in slightly deeper waters to the west (Fig. 3.1). Many of these foraging hotspots were in relatively shallow and flat areas (Table 3.1). Foraging in shallow waters allows shags to remain at the bottom phase of their dive longer, which has been shown to increase capture rate, improving dive efficiency (Wanless *et al.*, 1993). Our lack of evidence for an effect of bathymetry on foraging effort (as measured by the summed FPT within a hotspot) is likely due to the low levels of variation between these foraging hotspots. Birds from both colonies foraged most frequently in the narrow channels between islands (Fig. 3.3), mostly returning to a small number of sites. Similar levels of site fidelity have also been found in other populations of shags (a

study in the Isle of May estimating that less than 11% of available foraging areas were used (Wanless, Harris & Morris, 1991)) and related species, such as the pelagic cormorant *Phalacrocorax pelagicus* (Kotzerka *et al.*, 2011).

Birds did not travel far from their home colonies to forage, though birds from Annet (the largest colony) travelled slightly further (Table 3.1). The foraging ranges of birds from Samson were also more likely to overlap those of birds from Annet (Fig. 3.2), suggesting that shags from this colony might travel further to access the same foraging areas as birds from Samson. The bird from the Ganinicks also travelled short distances and foraged in similar areas to birds from Samson (Fig. 3.1). These findings differ somewhat from some other studies of shags, which suggest slightly longer foraging ranges. On average, Isles of Scilly shags travelled 1.7 km compared to shags breeding in Wales (average distance 12 km, Rees, 1965) and North-East Scotland (average distance 8 km, Elkins & Williams, 1974). The reason for these differences is unclear, though earlier studies were not based on GPS tracking. More recent studies found that shags breeding on Puffin Island, Wales travelled an average of 5.6 km to forage (L. M. Soanes pers comm., Soanes *et al.*, 2014) while birds from the Isle of May travelled an average distance of 9 km (Bogdanova *et al.*, 2014). Differences in foraging ranges may be due to prey availability, habitat suitability, intraspecific competition, or a combination of these factors (Birt *et al.*, 1987; Votier *et al.*, 2011).

One of the main theoretical requirements for information transfer at a colony is that prey is patchy and ephemeral (Ward & Zahavi, 1973b). The close proximity of shag foraging grounds to the colony make it unlikely that shags engage in the information transfer at colonies observed in related species (Weimerskirch *et al.*, 2010). A lack of information transfer at the colony would also explain the high

degree of overlap in foraging areas, rather than the colony-specific or even sub-colony specific differences in foraging areas found in other multi-colony studies of seabird species (Bogdanova *et al.*, 2014; Sapoznikow & Quintana, 2003; Wakefield *et al.*, 2013b; Wanless & Harris, 1993). It has been suggested that such segregation may be due to social information transfer at the colony, leading to differing search tactics between colonies (Wakefield *et al.*, 2013b). If shags mainly rely on memory and local enhancement, it is unlikely these differences will arise (Danchin *et al.*, 2004). Alternatively the lack of differences between colonies may be due to the comparatively smaller scales at which shags forage. Despite the apparent low value of conspecific foraging information, many foraging trips were made to areas where rafts form frequently (Table 3.1; Fig. 3.1) and large groups were frequently seen commuting from colonies to form foraging rafts. This may be due to birds utilising the same predictable sources of prey and attempting to reduce interference (Barnard *et al.*, 1982; Hoffman *et al.*, 1981). Alternatively foraging rafts may confer advantages to individuals such as reduced individual risk (Roberts, 1996), enhanced predator detection (Beauchamp, 2001; Cresswell, 1994) or increased foraging intake (Dermody *et al.*, 2011; Templeton & Giraldeau, 1995). It may therefore be advantageous to forage close to a colony to increase opportunities of being recruited to foraging rafts.

As the vast majority of shags are concentrated within inshore waters in close proximity to breeding colonies, this population may be particularly vulnerable to environmental impacts. This will likely be the case with other seabird species which forage within inshore waters, and damage to coastal habitats could force these species to make longer commuting flights which may have consequences for fitness (Davoren & Montevecchi, 2003).

In conclusion, our study shows how shags utilise their habitat by using high resolution GPS tracking and observations of group foraging behaviour. We discover clear patterns in the foraging behaviour of shags which differ from those observed in other species. These patterns emphasise the importance of the Isles of Scilly as a resource for seabirds and may indicate areas within the islands that are particularly important for shags during the breeding season. This study also suggests that while it seems unlikely that shags utilise social information at the colony they may use it while feeding in groups at the foraging patch. Understanding how these different types of information transfer might interact and affect foraging behaviour will be important in future studies of inshore foraging seabird species. Similarly further study of foraging rafts and the behaviour of individuals within them would help clarify the mechanisms that lead to the formation and maintenance of these assemblages.

4. The natural history of raft diving by European shags



4.1 Abstract

Much research has examined the behavioural and physiological requirements that enable air breathing diving animals to maximise prey intake. However, far less is known about the impacts of social interactions on diving behaviour. In this paper we examine how environmental conditions affect the formation and distribution of large foraging rafts of European shags (*Phalacrocorax aristotelis*) and how these relate to the type advantages diving in groups might bring. Observations of shags in waters around the Isles of Scilly reveal that raft size is affected by changes in sea state and tide. Rafts were larger at lower tidal heights, especially during low tidal flows. Our results provide new insight into the possible benefits of social diving in this species, with a number of ecological and applied implications. Therefore our work highlights the significance of social interactions for understanding diving behaviour and suggest this under-studied area may be the subject of fruitful future research.

4.2 Introduction

Air breathing animals that dive for food face enormous challenges while foraging. Not only do they have to find, pursue and catch their prey in an unpredictable environment, but they must do it while under the physiological constraint of holding their breath (Butler & Jones, 1997). As a result they must balance the complex tasks of optimising time spent foraging underwater with the need to regain oxygen on the surface, while at the same time minimising the costs of overcoming neutral buoyancy (Ydenberg & Clark, 1989a). There have been numerous empirical studies investigating various aspects of diving behaviour. Physiological experiments have examined how factors such as metabolic rate and oxygen storage can affect an animal's ability to remain submerged for extended periods of time (MacArthur & Krause, 1989). Other studies have investigated the

behavioural decisions animals must make while diving, such as the depth, frequency and length of dives (Cook *et al.*, 2012; Hanuise, Bost & Handrich, 2013; Mori, 1998). Additional behavioural studies focus on what factors and conditions might influence an animal's choice of where to dive and how that choice might affect decisions made at the patch (Brandt, 1984; Mori *et al.*, 2002). A large number of theoretical models have also been developed, examining how differing diving strategies will affect fitness and exactly what constitutes an optimal dive (Mori, 1999; Ydenberg & Clark, 1989a). Knowing how these components combine to affect diving efficiency is vital in our understanding of the life-styles of air breathing diving animals. However, the vast majority of these studies deal with solitary animals (But see: Anderson, 1991; Beauchamp, 1992; Lukeman *et al.*, 2010a; Schenkeveld & Ydenberg, 1985b), despite the fact that many species dive in groups (Bearzi, 2006; Irons, 1998; Lacroix *et al.*, 2005; Takahashi *et al.*, 2004b).

Animals diving in groups share many of the same costs as group foragers in terrestrial environments including increased competition (Foster, 1985; Ranta *et al.*, 1993), interference (Ruxton, 1995), kleptoparasitism (Ranta *et al.*, 1993) and predator attraction (Cresswell, 1994). Moreover, underwater interference or collisions can be particularly problematic for diving animals (Cairns, 1992; Machovsky Capuska *et al.*, 2011). These costs must be outweighed by the benefits provided by foraging in a group in order to make this behaviour evolutionarily stable. Among the numerous suggested advantages are reduced individual risk (Roberts, 1996), enhanced predator detection (Beauchamp, 2001; Cresswell, 1994), resource access (Dall & Wright, 2009a), and increased foraging efficiency (Bednarz, 1988). Group diving animals might increase foraging efficiency by gaining hydrodynamic benefits from diving together, reducing the energetic costs of diving (Noren *et al.*, 2006) or by

herding fish, forcing prey into areas where they can be more easily exploited (Benoit-Bird & Au, 2009). Social information from diving conspecifics might also allow individuals to improve foraging efficiency (Dermody *et al.*, 2011; Templeton & Giraldeau, 1995). Making a dive involves a significant investment in time and energy (Williams & Yeates, 2004) such that selection should strongly favour efficient foraging. As such, these behaviours, where conspecifics might display a high degree of alignment, polarity and synchronicity of diving (Beauchamp, 1992; Berlincourt & Arnould, 2014; Schenkeveld & Ydenberg, 1985b), can be distinguished from simple aggregative behaviour where individuals form large groups via conspecific attraction and attempt to exploit the same food source. These aggregations are usually disorganised and involve a high degree of intraspecific kleptoparasitism (Barnard *et al.*, 1982; Hoffman *et al.*, 1981). The coordination observed from social diving must therefore confer additional benefits than those derived when every individual is simply trying to access the same resource at once.

Diving in groups requires a sufficient abundance of prey to support a large number of animals and may therefore be expected to occur only in certain areas (Heithaus, 2005). It might also occur if animals are forced to aggregate in certain areas by restrictions on the number of available foraging locations (Hilton, Ruxton & Cresswell, 1999). However the advantages mentioned might improve animals' ability to exploit certain locations more effectively than they would if they were alone (Battley *et al.*, 2003). Similarly, hydrodynamic or information benefits could allow animals to forage in hostile conditions such as rough seas or potentially high-risk locations such as areas of high tidal flow or dangerous physical features. This could lead to group diving behaviour being concentrated in certain areas, and animals

displaying behavioural plasticity in switching between solitary and group diving under certain conditions.

Many aquatic birds frequently engage in group diving, forming large flocks (hereafter referred to as “foraging rafts”) while foraging. These foraging rafts consist of anywhere between five to several hundred birds moving along the surface of the water and diving together, displaying a high degree of cohesion and alignment. These formations have been observed in surf scoters *Melanitta perspicillata* (Lukeman *et al.*, 2010a; Schenkeveld & Ydenberg, 1985b) and Barrow’s goldeneyes *Bucephala islandica* (Beauchamp, 1992), American White Pelicans *Pelecanus erythrorhynchos* (Anderson, 1991) and numerous *Phalacrocorax* species (Nelson, 2005). Foraging rafts differ from other similar assemblages, such as the compass rafts formed by Guanay cormorants *Phalacrocorax bougainvillii* (Weimerskirch *et al.*, 2010) since the latter aggregations are not associated with foraging (Furness, Hilton & Monteiro, 2000; Wilson *et al.*, 2009). In this study we investigate the location and environmental conditions under which group diving occurs in a wild population of European Shags *Phalacrocorax aristotelis* (hereafter ‘shag’). European Shags are colonial breeding, pursuit diving seabirds. They forage in sandy, rocky areas at depths of up to 40 metres both solitarily and in foraging rafts, feeding mainly on small fish such as sandeels (Anker-Nilssen, 2009; Nelson, 2005). We predict that when and where these rafts occur will depend heavily on tidal conditions, sea state and weather conditions. We predict that larger rafts will be focused in flat, shallow areas where prey is abundant, most likely when tidal height is low (Macer, 1966). If rafting provides hydrodynamic benefits, reducing the energetic cost of diving, we predict rafts will form in adverse tidal conditions in which diving requires increased effort such as fast tidal flow during high tides. If birds benefit from social information while

diving in groups, we may expect that rafts will be larger when social information is more valuable such as in rough sea conditions (high windspeed, fast flowing low tides). These conditions may increase the difficulty of keeping track of the distribution of prey underwater, making social information from conspecifics more valuable (White *et al.*, 2007). We hope to gain new insight into the conditions that cause these groups to form and the nature of the advantages that diving air breathers might obtain from social diving behaviour.

4.3 Methods

4.3.1 Fieldwork

Fieldwork was carried out on the Isles of Scilly (49.9361° N, 6.3228° W). Observations of rafting birds were made from the islands of St Marys and St. Agnes between from 3/5/13 to 8/7/13 and again from 1/5/14 till 1/6/14. We collected data throughout an entire lunar tidal cycle including spring and neap tides. The circumferences of the two islands were divided into transects of roughly equal length, six on St Marys and three on St Agnes. Each of these transects contained six observation points. Transects lasted two hours in total, with observers spending 15 minutes at each observation point. Three transects were carried out daily, from 8:00 - 10:00, 11:00 - 13:00 and from 14:00 - 16:00. For each time of day data were recorded at tidal ebb and flood and at three different speeds of tidal flow, based on the rule of twelfths (A method for estimating tidal flow, assuming that during a 6-hour tidal range the tide rises or falls in twelfths of its range in the pattern: 1, 2, 3, 3, 2, 1). The transects visited each day were pseudo-randomly selected, based on what combinations of site, tidal state and time of day had previously been sampled and walked in a random direction. When a raft consisting of at least five birds was

spotted, the GPS coordinates of where the observer was standing were recorded (eTrex Summit® HC, Garmin Ltd.). Raft movements were recorded until the raft dispersed or was out of sight. During observations, each raft was filmed continuously using a video camera (Sony Handycam HDR-CX190E, Tokyo, Japan). Bearings of the raft relative to magnetic north were taken every five minutes using a compass or more frequently if shags flew from one location to another. In this case the bearing at the beginning and end of the flight event were recorded. Raft size was recorded every five minutes, unless the raft underwent a sudden significant change in size (i.e. a smaller raft/flight of >20 birds joined the observed raft). Birds were counted as being part of a raft if they were within five body lengths of the main assemblage. The number of individual birds in a raft was counted up to a 100 individuals, after which birds were counted in groups of 10. If a raft split into multiple smaller rafts, the largest continued to be tracked.

4.3.2 Data processing and kernel estimation

Bearings were plotted as lines from the observation point using ArcGIS (ESRI, 2012). A 3d representation of the Scillies (Terrain data acquired from Ordnance Survey Land-Form PROFILE dtm dataset (2009) , detailed charts acquired from SeaZone Solutions HydroSpatial One dataset (2015)) which was matched with the video footage using ArcVIEW and used to estimate distance along the bearing, allowing us to plot the location of rafts within the islands (Fig. 4.1). To quantify where in the islands rafts regularly form, positions of rafts where birds were on the water were used to calculate a utilisation distribution (UD) kernel estimation (Fig. 4.2)(Worton, 1989) using the R package, adehabitatHR (Calenge, 2006), in R 3.1.1 (R Core Team, 2014). A similar UD kernel estimation with positions weighted by the number of individuals within a raft was also created, to investigate if larger rafts

formed in certain locations (Fig. 4.3). Each observation was assigned appropriate environmental, tidal and weather conditions. Median bathymetry and median slope of bathymetry were extracted from each location. Tide conditions assigned included the tidal height and the estimated speed and direction of tidal flow at surface. Tidal height between high and low tides and the speed of tidal flow were calculated according to the rule of twelfths (A method for estimating tidal flow, assuming that during a 6-hour tidal range the tide rises or falls in twelfths of its range in the pattern: 1, 2, 3, 3, 2, 1). Weather data were obtained from the UK Met Office and included wind-speed, wind direction and visibility. To aid in analysis, the wind directions were categorised as north, east, south or west, according to closest compass direction. Similarly, the areas rafts were seen in were recategorised as North East, South West and North West of St. Mary's and North West of St. Agnes (no rafts were observed South East of St Mary's or St. Agnes).

4.3.3 Statistical analyses

Statistical analyses were carried out using linear mixed effects models that included an exponential spatial autocorrelation structure. Three main models with raft size as the response variable were considered. In all models, raft size was square-root transformed to satisfy assumptions of normality. To maximise model accuracy we excluded the few extremely small (<5) and extremely large (>350) raft sizes. Raft ID was fitted as a random effect in all models due to their being multiple observations of each raft. The first model considered how the size of rafts might differ depending on by tidal conditions. Raft size was fitted as a function of site, tide height, tidal flow, tide direction, bathymetric depth and bathymetric slope. The second model examined how raft size can be affected by sea state. For this model, raft size was fitted as a function of site, wind speed, wind direction, tidal flow, tidal

height, tide direction and bathymetric depth. Finally we used a simple model to examine if site use varied over time. For this we fitted raft size as a function of site and date. In all models, all possible combinations of fixed effects and their 2-way interactions were considered. Measures of visibility, wind speed, bathymetry, bathymetric slope, tidal height and tidal flow were grand mean centred (Hofmann & Gavin, 1998). This was done so as to make model estimates of these effects easier to interpret. All models were run using the R package nlme (Pinheiro *et al.*, 2014). The best models were selected using Akaike's second order Information Criterion (AIC, Burnham & Anderson, 2002) using the R packages MuMin (Bartoń, 2014).

4.4 Results

In total 95 rafts of foraging shags were recorded, with approximately a maximum size of 520 birds and an average size of 177 ± 116 SD. Rafts only formed within the main channels between the islands, no rafts were seen on the eastern side of the islands, outside of the shallow waters that surround the Scillies (Mean bathymetry: 2.97 ± 5.42 SD metres below lowest astronomical tide, Fig. 4.1), though bathymetry was not found to have an effect on raft size. The largest rafts formed consistently and frequently in the shallows in the North-East of the islands (North West of St. Mary's), throughout the study periods in both years (Fig. 4.3, Table 4.1).

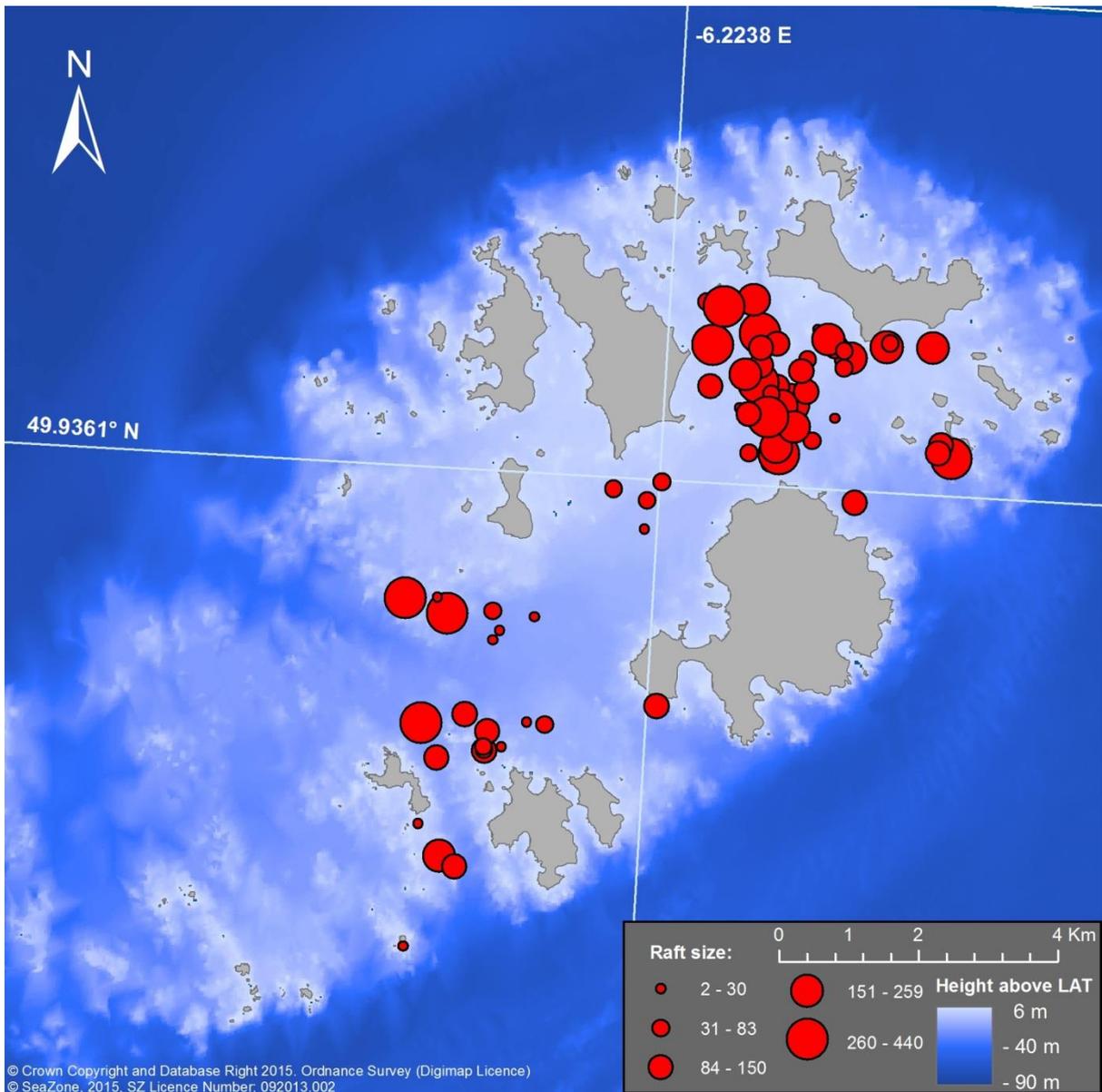


Figure 4.1: Distribution of observed foraging rafts of European shags in comparison to bathymetry. Size of symbol represents number of birds in a raft. LAT=Lowest astronomical tide.

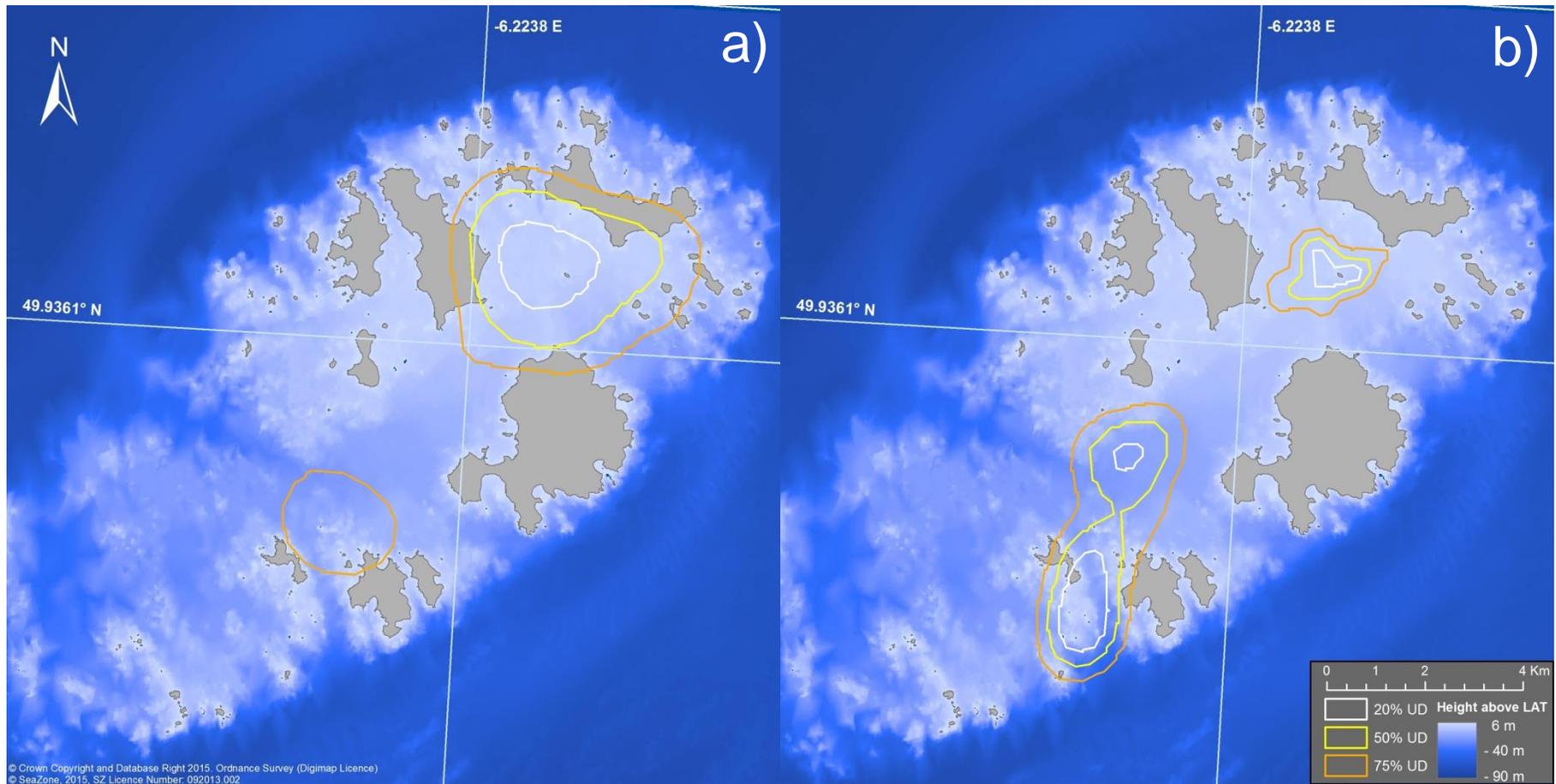


Figure 4.2: Distribution of observed foraging rafts of European shags in a) 2013 and b) 2014. Lines indicate 75, 50% and 20% contours of Utilization Distribution (UD) from Kernel analysis. LAT=Lowest astronomical tide.

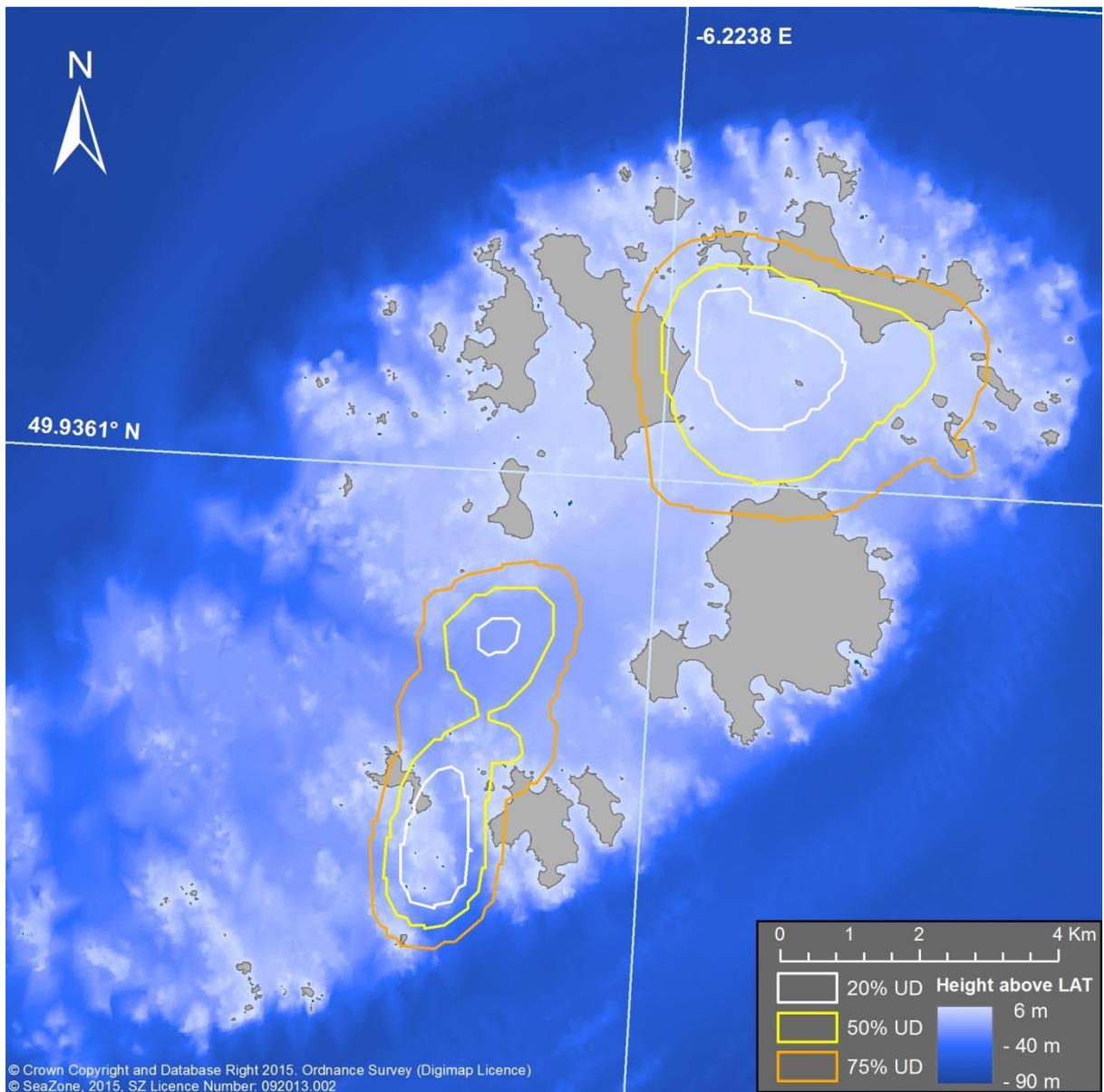


Figure 4.3: Distribution of observed foraging rafts of European shags weighted by raft size in comparison to bathymetry. Lines indicate 75, 50% and 20% contours of Utilization Distribution (UD) from Kernel analysis. LAT=Lowest astronomical tide.

Table 4.1: Summaries of the top models for each model type (tide, sea state and weather) including $\Delta AICc$ from the full models.

Model type	$\Delta AICc$	Response	Fixed effect	Estimate	$\pm S.E$	d.f			
Tide	85.97	sqrt(Raftsize)	intercept	7.87	0.89	395			
			Tide height	-0.15	0.11	395			
			Speed of tidal flow	-0.64	0.46	395			
			Direction of tidal flow (Ebb)	1.65	0.61	395			
			Site (NE)	2.68	1.08	395			
			Site (SW)	0.49	1.05	395			
			Site (NW)	3.16	1.07	395			
			Tide height x Speed of tidal flow	-0.67	0.20	395			
			Direction of tidal flow (Ebb) x Speed of tidal flow	1.71	0.65	395			
			Speed of tidal flow x Site (NE)	-1.32	0.71	395			
			Speed of tidal flow x Site (SW)	-1.20	0.98	395			
			Speed of tidal flow x Site (NW)	-1.66	0.68	395			
			Sea State	44.84	sqrt(Raftsize)	intercept	5.72	3.15	375
						Speed of tidal flow	-0.48	1.30	375
Tide height	0.09	0.11				375			
Direction of tidal flow (Ebb)	3.43	1.29				375			
Site (NE)	4.87	3.16				375			
Site (SW)	6.59	3.94				375			
Site (NW)	5.42	3.15				375			
Wind Direction (E)	1.23	3.39				375			
Wind Direction (S)	2.92	3.35				375			
Wind Direction (W)	3.63	3.35				375			
Speed of tidal flow x Site (NE)	-1.47	1.01				375			
Speed of tidal flow x Site (SW)	0.83	2.11				375			
Speed of tidal flow x Site (NW)	-0.43	1.04				375			
Tide height x Speed of tidal flow	-0.43	0.18				375			
Direction of tidal flow (Out) x Speed of tidal flow	1.34	0.74				375			
Speed of tidal flow x Wind Direction (E)	0.17	1.11				375			
Speed of tidal flow x Wind Direction (S)	3.63	1.29				375			
Speed of tidal flow x Wind Direction (W)	0.16	1.10				375			
Site (NE) x Wind Direction (E)	-0.95	3.33				375			
Site (NE) x Wind Direction (S)	-2.55	3.88				375			
Site (NE) x Wind Direction (W)	-3.74	3.32				375			
Site (SW) x Wind Direction (E)	-6.81	4.39				375			
Site (SW) x Wind Direction (S)	-10.60	4.62				375			
Site (SW) x Wind Direction (W)	-6.94	4.22				83			
Site (NW) x Wind Direction (E)	-1.15	3.36				375			
Site (NW) x Wind Direction (S)	-2.27	3.88				375			
Site (NW) x Wind Direction (W)	-3.58	3.31				375			
Direction of tidal flow (Out) x Wind Direction (E)	-0.59	1.28				375			
Direction of tidal flow (Out) x Wind Direction (S)	-3.16	1.46				375			
Direction of tidal flow (Out) x Wind Direction (W)	-0.29	0.95				375			
Direction of tidal flow (Out) x Site (NE)	-2.93	0.95				375			
Direction of tidal flow (Out) x Site (SW)	-0.25	1.18				375			
Direction of tidal flow (Out) x Site (NW)	-3.41	0.93				375			

4.4.1 Tide

Raft size was related to interactions between the speed and direction of tidal flow (Fig. 4.4, Table 4.1). When the tide was ebbing (i.e. the outgoing tide), rafts were larger at higher tidal flows. When tide was flooding (i.e. the incoming tide), rafts were smaller at higher tidal flows. Raft size was also found to be affected by the interaction between the speed of tidal flow and the tidal height (Fig. 4.5, Table 4.1). Rafts were larger when tidal flow was faster at lower tidal heights. Rafts around St Mary's were slightly smaller at higher flow speeds than those North West of St. Agnes (Table 4.1)

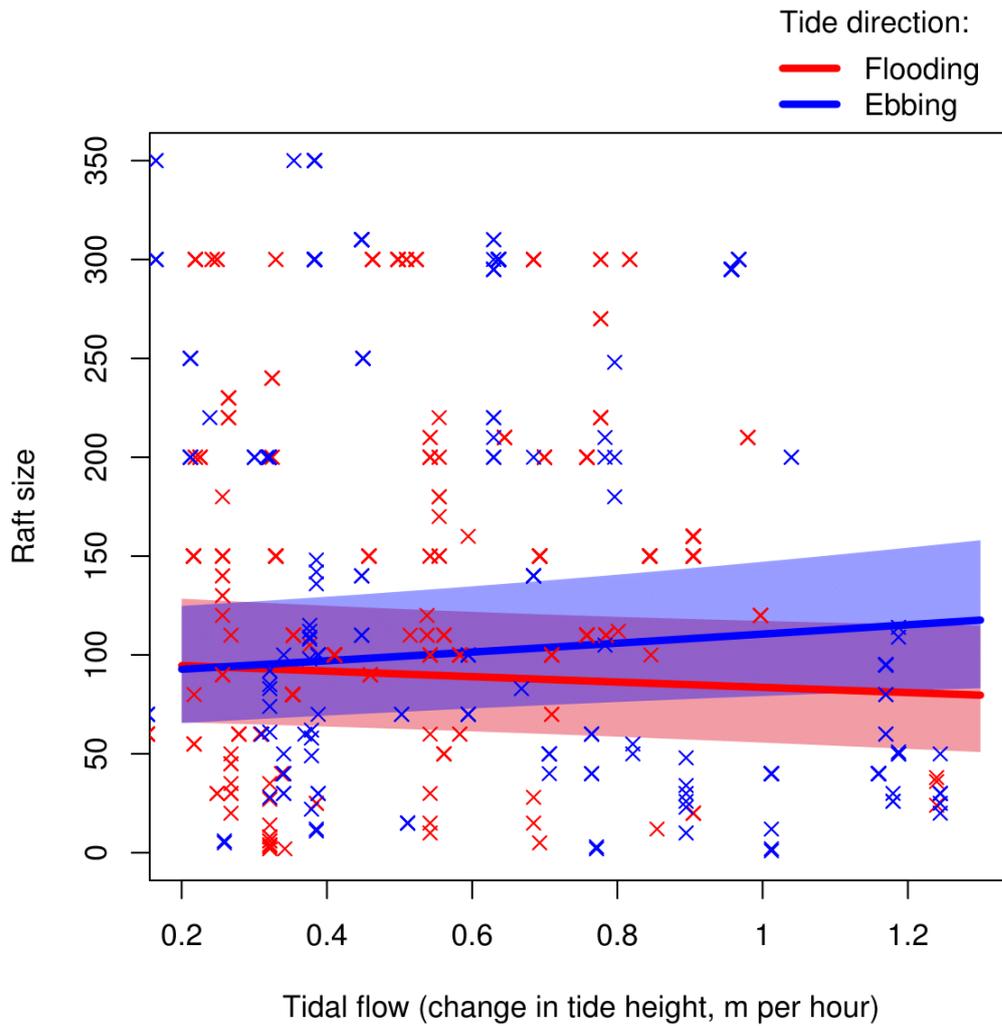


Figure 4.4: Model estimate plot showing the small effect of the interaction between tide direction and speed of tidal flow on average raft size at all sites, with standard errors. Red represents a flooding tide while blue is an ebbing tide.

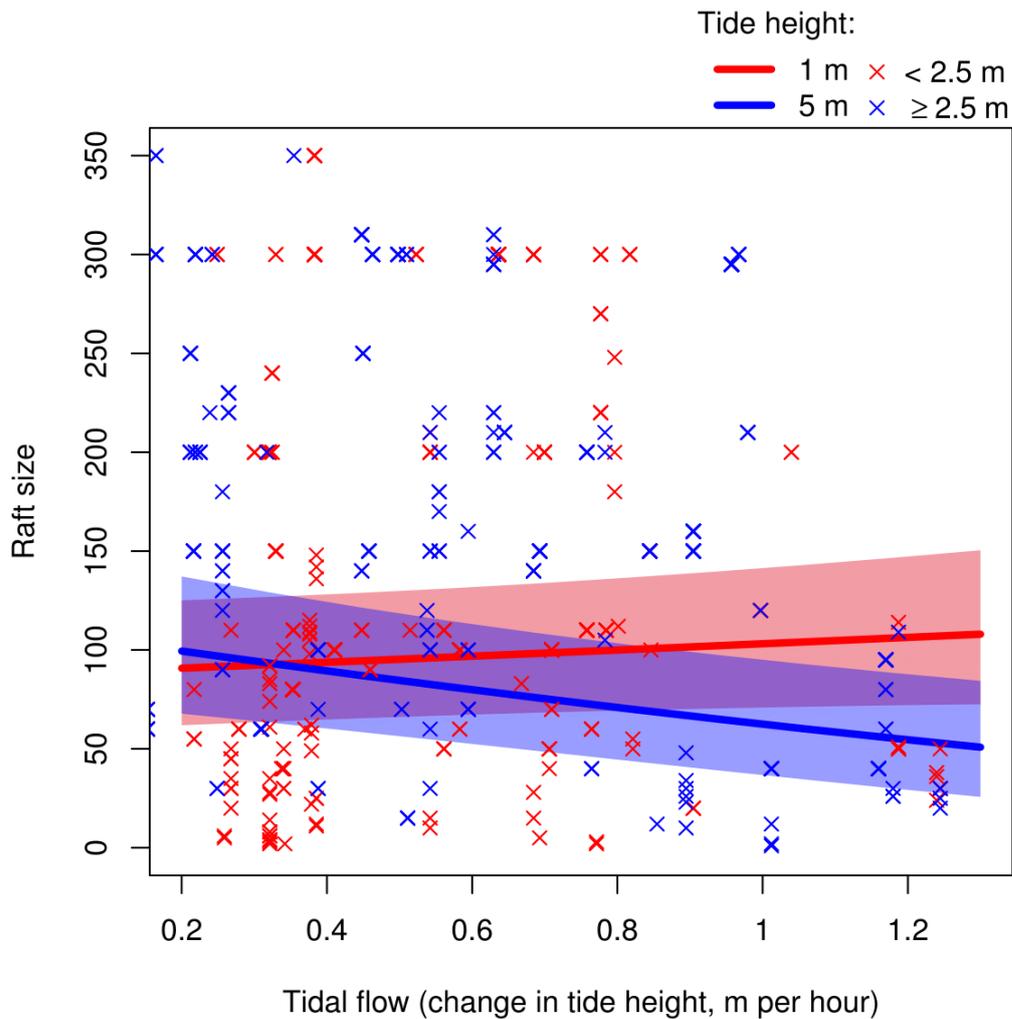


Figure 4.5: Model estimate plot showing the effect of the interaction between tide height and speed of tidal flow on the average raft size for all sites, with standard errors. The red line represents the effect of tidal flow when tide height is 1 m while the blue line is a represents the effect of tidal flow when tide height is 5 m. Datapoints are red where tide height was <2.5 and blue where tide height was ≥ 2.5 .

4.4.2 Sea state

Raft size was found to be influenced by the interaction between speed of tidal flow and wind direction (Fig. 4.6, Table 4.1). Raft size was also affected by direction of tidal flow interacting with the speed of tidal flow and direction of tidal flow (Fig. 4.6, Table 4.1). When the tide was ebbing raft size remained fairly constant at faster tidal flows when wind was blowing from the West, North or East. When the wind blew from these directions and tide was flooding, raft size

decreased with flow speed (Fig. 5). When the wind blew from the south however, raft sizes increased at faster speeds of tidal flows, in both tide directions (Fig. 4.6), though this effect was reduced for rafts forming to the South West of St. Mary's (Table 4.1).

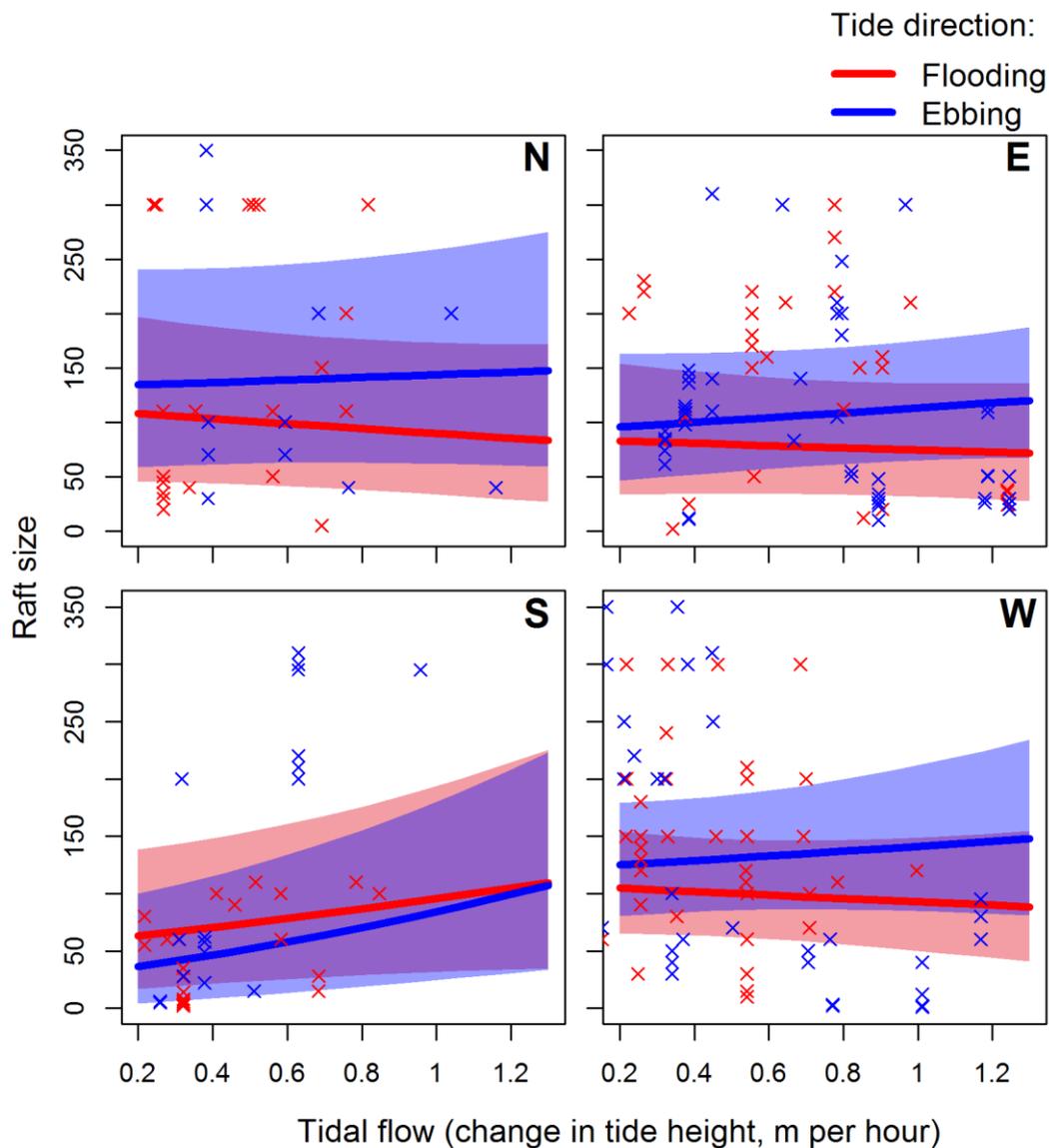


Figure 4.6: Model estimate plots showing the effect of the interaction between wind direction and speed of tidal flow and the interaction between wind direction and direction of tidal flow on the average raft size for all sites, with standard errors. Blue is an ebbing tide while red is a flooding tide.

4.4.3 Site consistency

Neither date nor the interaction between date and site was found to have an effect on raft size, with raft sizes remaining consistent in all sites throughout the period of study.

4.5 Discussion

This study presents the first systematic investigation into the rafting behaviour of European Shags. The formation and size of rafts was found to be affected by a combination of tidal conditions and sea state (Fig. 4.4, 4.4, 4.5), and focused in specific locations within the isles of Scilly (Fig. 4.1, 4.3, Table 4.1). These results suggest that changing tide and sea state alter the costs and benefits of foraging in rafts. Below we offer potential explanations for the behaviours observed and what these findings entail about shag foraging rafts and social diving in general.

The largest observed rafts were concentrated in shallow waters (<4.5 m below lowest astronomical tide) roughly in the centre of the archipelago (Fig. 4.3, Table 4.1). These locations are presumably sufficiently rich in fish to support the large numbers of foraging birds observed. Tidal flow through channels between islands may cause easily exploitable prey accumulations to form (Holm & Burger, 2002; Hunt, 1991; Irons, 1998). Turbulent areas such as these channels are also a favoured habitat of sandeels (*Ammodytes spp.*), one of the main prey items of shags (Macer, 1966; Reay, 1970) which are frequently found in the islands and thought to be of great importance to the local seabird populations (commercial fishing of the species is banned within the islands, Inshore Fisheries and Conservation Authority, 2011; Natural History Museum, 2014). Sandeels prefer shallow, flat, sandy areas, characteristics which the

areas where rafts frequently formed share. Despite this, the size of rafts did not differ with bathymetry, perhaps because bathymetry varied little in the main study areas (Evans, Dall et al. in review). The location and bathymetry of these areas makes fish herding behaviour unlikely as this usually requires natural barriers such as a rocks, a shoreline or extremely shallow waters (Anderson, 1991). While many rafts were observed in close proximity to beaches, there was no indication that fish were being driven towards the shoreline.

The locations where the largest rafts formed were in close proximity to rocks where large numbers of shags regularly perch (Fig. 4.3, Table 4.1). Synchronous departures from these rocks were regularly observed, with large groups of birds leaving the rock to form rafts. The close proximity of regular rafting sites and the general predictability of shag foraging behaviour within the isles of Scilly make it unlikely that birds follow each other to find unknown foraging patches (Evans, Dall et al. in review). However, shags may follow each other due to the advantages conferred by diving in a group, making these perches recruitment centres (Richner & Heeb, 1995). Alternatively the short distance from these rocks to rafting areas might suggest a simple conspecific attraction effect, with birds leaving their perches to join an existing raft (Buckley, 1997a) though this requires an aggregation to have already formed and does not explain synchronous departures.

Though raft sizes did not vary with bathymetric depth, rafts were larger at lower tidal heights, especially when speed of tidal flow was high (Fig. 4.5). If shags are feeding on benthic fish like sandeels, lower tide heights would require less travelling time during dives allowing them to remain at the bottom longer, increasing capture rates and improving dive efficiency (Raya Rey *et al.*, 2010;

Wanless *et al.*, 1993). The larger rafts observed as flow speed increased may indicate that there is some benefit to foraging in faster tidal flows during lower tides, possibly due to increased prey availability (Holm & Burger, 2002). During higher tides, raft size decreased during faster tidal flows (Fig. 4.5). Possibly increased effort is required to dive in these conditions, which reduces foraging efficiency (Finney, Wanless & Harris, 1999). If this is the case, these results suggest that foraging rafts do not allow individuals to counteract this through any hydrodynamic benefits gained from social diving.

During a flooding tide, raft sizes were smaller at higher tidal flow speeds (Fig. 4.4), but when the tide was ebbing, this effect was reversed. This is possibly linked to the movement of prey during a tidal cycle. Prey may be brought closer to shore during a flooding tide, making slack tides the optimum time to forage after the tide has risen (Corkhill, 1973; Jovanovic *et al.*, 2007). As tide ebbs prey will be required to migrate to deeper waters, forcing them from hiding (Bretsch & Allen, 2006; Gibson, 2003). Faster flow speeds may therefore lead to a greater abundance of prey present in the water column when the tide drops more quickly (Raya Rey *et al.*, 2010), allowing large aggregations to form, which can enable social diving.

Rafts were larger at higher tidal flows when the wind blew from the south (Fig. 4.6, Table 4.1). Southerly winds might interact with faster tidal flow speeds to create inhospitable conditions in the main channel between islands (Lapworth, 2011). This may restrict the number of viable foraging locations both inside and outside the islands, forcing birds into more sheltered waters closer to the shore (Finney *et al.*, 1999). This would also explain why this effect appeared to be reduced for rafts forming in the less sheltered waters to the South West of

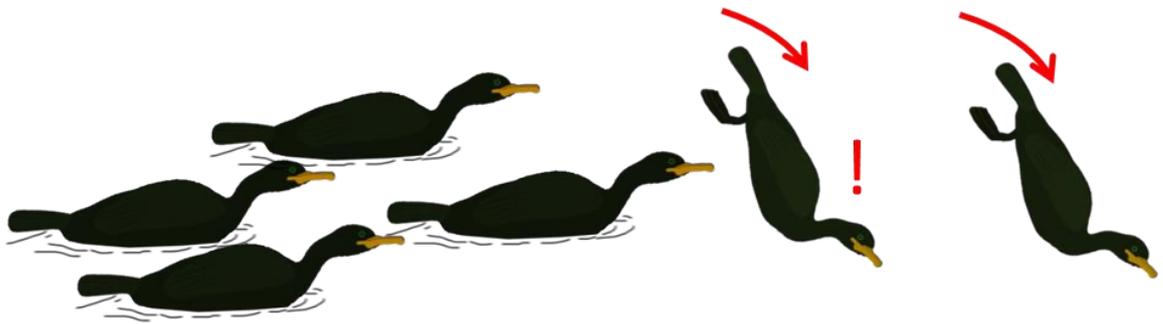
St. Mary's (Table 4.1). As before, while lack of alternative foraging areas can explain basic aggregation, it is insufficient to explain the formation of coordinated foraging rafts (Battley *et al.*, 2003).

4.6 Conclusions

Here we provide the first detailed description of the environmental conditions associated with the formation of large rafts of socially diving birds. While these results provide some insight into the advantages individuals might gain from diving in a group, there is still considerable uncertainty about the proximate mechanisms influencing collective behaviour. Predation risks to adults are minimal in this population, meaning that anti-predation benefits are unlikely to be a suitable explanation for group foraging. While the location and timing of rafting events relative to weather and tide condition seem to indicate that aggregation of prey enables the formation of foraging rafts, these alone are an insufficient explanation. This suggests that while the costs and benefits of grouping are altered by tide and sea state, there are likely to be other benefits to be obtained by individuals group foraging in this system, which may include increased opportunities to copy dive behaviour or gain social information about the location or prey. Greater insight into potential benefits might be obtained using a more detailed four-dimensional dataset of water flow within the islands, which would allow more accurate modelling of the influence of varying tide and sea state on group formation. Carrying out similar studies in other group diving species especially species which are known to herd fish or suffer predation could also provide a useful contrast to these results and aid in differentiating between conditions that allow aggregation and the advantages individuals gain from diving within an aggregation. Ultimately it will be necessary to utilise high resolution data of movement and diving behaviour in order to understand how

important these advantages may be to individuals diving within groups, which will shed light on how individual benefits contribute to the establishment and behaviour of groups of socially diving animals.

5. The use of social information while diving in groups: a dynamic programming approach



5.1 Abstract

Group foraging is a common tactic among a wide range of taxa. Most studies have focussed on this behaviour in terrestrial environments with much less known about group foraging among air breathing aquatic animals. Here we study social information use in a hypothetical diving air-breathing animal. Using dynamic programming, we investigate the optimal decisions of an animal diving in a group depending on environmental conditions, number of neighbours, the nature of prey and an animal's ability to judge the foraging success of conspecifics. We show that copying the dive behaviour of others is beneficial, even when choosing a neighbour to copy at random. We found that copying dive behaviour of a conspecific is usually the optimal strategy, unless overridden by an individual's personal information. The prevalence of dive copying behaviour was therefore highly dependent upon the length of time that an animal's personal information remained up to date. These findings suggest that using the behaviour of conspecifics to inform their own diving behaviour can be beneficial for diving animals, and therefore hint at the ecological factors driving group diving behaviour in air-breathing aquatic animals.

5.2 Introduction

Foraging in groups is common among a taxonomically diverse range of animal taxa (Foster, 1985; Inger *et al.*, 2006; le Roux *et al.*, 2009). Group foraging can provide numerous benefits such as decreased predation risk (Roberts, 1996) and increased foraging efficiency (Bednarz, 1988), but individuals within the groups will also suffer increased competition (Foster, 1985; Ranta *et al.*, 1993), interference (Ruxton, 1995), kleptoparasitism (Ranta *et al.*, 1993) and predator attraction (Cresswell, 1994). Much research has examined the potential evolutionary advantages that drive non-kin group

foraging (Clark & Mangel, 1986; Elgar, 1989; Roberts, 1996) in terrestrial systems, but far less attention has been paid to group dive behaviour in aquatic animals (Elgar, 1989). Air breathing animals that dive for food face additional complications while foraging as they have to find, pursue and catch prey while holding their breath (Butler & Jones, 1997). The physiological and behavioural requirements for a single animal to maximise prey intake underwater have been examined in numerous studies, but comparatively little work has been carried out on group diving species (Heithaus & Frid, 2003; Mori *et al.*, 2002). Many species dive in large groups, often displaying a high degree of alignment, polarity and synchronicity of diving (Beauchamp, 1992; Berlincourt & Arnould, 2014; Schenkeveld & Ydenberg, 1985b). It can be assumed that in order for this type of group diving behaviour to be viable, it must confer more benefits than every individual simply trying to access the same resource at once.

Diving for food in a group bestows many of the same benefits as group foraging in a terrestrial environment, but may also confer additional benefits, such as increasing foraging efficiency using fish herding behaviour or reducing energetic costs via hydrodynamic benefits (Benoit-Bird & Au, 2009; Noren *et al.*, 2006). Making a dive can also require a high investment in time and energy and, depending on environmental conditions, keeping track of the location and distribution of prey underwater can be challenging (White *et al.*, 2007). As making an informed dive will be vital for efficient foraging, information about the location of food underwater will be extremely valuable to diving animals (Schmidt, Dall & Van Gils, 2010a; Williams & Yeates, 2004). By diving in groups, individuals may benefit from easy access to social information about prey distribution from conspecifics and possibly enhance foraging efficiency by observing and copying the diving behaviour of more informed conspecifics

(Coolen *et al.*, 2003; Dall *et al.*, 2005b; Rands *et al.*, 2003; Rands *et al.*, 2004; Valone, 2007).

How often individuals might copy dive behaviour will depend on the value of social information about prey, which will be affected on factors such as the number of individuals within a group, environmental conditions (such as sea state or water clarity) and the distribution and behaviour of prey species (Eriksson, 1985; Rands *et al.*, 2004; White *et al.*, 2007). It may also be determined by an animal's ability to assess the foraging success of conspecifics (Coolen *et al.*, 2003; Rands *et al.*, 2003). In diving animals this can be difficult, especially if a species swallows its prey underwater. However studies have shown that in some situations it can still be beneficial to copy the behaviour of conspecifics, even if their foraging success cannot be determined conclusively (Rands *et al.*, 2003). Copying the diving behaviour of a conspecific will of course increase the likelihood of increased competition and interference underwater (Henkel, 2009; Ruxton, 1995). How important information use is as an advantage of social diving will be heavily dependent on the effectiveness of this strategy.

In this study we investigated the conditions that might affect a diving animal's use of social information from conspecifics. For this we used a stochastic dynamic programming model, based on a study by Ydenberg and Clark (1989) in which they investigate the diving decisions of western grebes (*Aechmophorus occidentalis*) based on their level of oxygen debt and their ability to find and keep track of prey. Stochastic dynamic programming models are computational techniques that find optimum sequences of actions. These methods are an ideal way to address the question of when to use social

information, as they allow a high degree of biological realism and the easy assessment of behavioural choices in terms of overall fitness (Clark & Mangel, 2000; Mangel & Clark, 1988). We examine how changes in environmental conditions, number of available neighbours and different prey types will affect an air breathing diving animals' decisions about when to rest, dive or copy a conspecific, giving new insight on how important easy access to social information will be to animals diving in groups.

5.3 Methods

The model was constructed using discrete-time dynamic programming. At each timestep t (approximately 30 seconds), to the end of potential foraging time T an animal must make a decision whether to rest, dive based on their own personal knowledge of prey location or attempt to dive using social information from a conspecific. Prey is assumed to be sufficiently abundant that the patch will never be depleted. The decision made will depend on which will maximize fitness, which is defined as the maximum expected catch of prey between t and T assuming an animal employs the optimum diving strategy. The fitness increase provided by each decision is calculated dependent on the values of four state variables, which are detailed in Table 5.1 and a selection of set parameters which are detailed in Table 5.2.

Table 5.1: Dynamic state variables

State Variable	Definition
t	Time (approximately 30 seconds)
X	Level of oxygen depletion
N	Number of timesteps since previous dive
S	1 if prey was encountered on previous dive otherwise 0

Table 5.2: Parameters used in model

Variable	Definition
c	Sea state: A value from 0 (best) to 1 (worst)
g	Group size (number of neighbours)
l	Base probability of encountering prey
r	Base probability of maintaining contact with prey
e	Base probability of capturing prey
h_0	Base probability of a chosen conspecific having encountered prey on previous timestep
h	Maximum probability of a chosen conspecific having encountered prey on previous timestep
x_1	Aerobic threshold
x_2	Anaerobic threshold
a_1	Aerobic diving cost
a_2	Anaerobic diving cost
b_1	Aerobic recovery rate
b_2	Anaerobic recovery rate
T	Terminal timestep.

5.3.1 Encountering prey

Two state variables N and S are used to determine the probability of encountering prey, λ .

$$\lambda(N, S) = \begin{cases} \max(\lambda_0^N, \mu) & \text{if } S = 1 \\ \mu & \text{if } S = 0 \end{cases} \quad (1)$$

Where μ is the probability of prey encounter for an uninformed individual and λ_0 is the probability of prey encounter of an informed individual. This probability varies depending on how accurate an animal's personal information about the location of prey currently is, with an animal that has encountered prey recently having a greater probability of encountering prey than an animal that has not encountered prey in some time, or not yet encountered prey. The probabilities of encounter μ and λ_0 are calculated as follows

$$\mu = c(1 - (1 - l)^{hg+1}) \quad (2)$$

$$\lambda_0 = c(1 - (1 - r)^{hg+1}) \quad (3)$$

Where g is group size (which represents effective number of neighbours), c is environmental conditions (representing sea state, visibility and any other aspects of the environment that might affect ability to find and catch prey) and h is an individual's ability to assess the foraging success of conspecifics. l is the base probability of encounter if an animal is uninformed and r if an animal is informed. These take into account the general ability of an animal to find prey depending on their own abilities, the difficulty of finding prey, prey distribution/density etc. (see Tables 5.2, 5.4). It is assumed that, even when an individual dives based on their personal information; larger numbers of neighbours will increase the probability of initially finding and then retaining contact with prey, due to their ability to use the presence of foraging conspecifics as cues about prey ability. This benefit is limited by poorer conditions and by an animal's own ability to judge the foraging success of their conspecifics.

5.3.2 Copying Behaviour

If an animal chooses to copy the dive behaviour of a conspecific, they have a probability σ of choosing to copy an informed individual. This value begins as h_0 (the base probability of choosing an informed conspecific with only 1 neighbour present) and assumed to increase when additional neighbours are

present (due to there being a higher number of individuals to choose from) up to a maximum of h . If an animal succeeds in choosing an informed neighbour, they are then assumed to have a λ_0 probability of encountering prey (the same value as if they had encountered prey themselves in a previous timestep). If an uninformed conspecific is chosen, an individual will have a μ probability of encountering prey (as though prey had not previously been encountered, as it is assumed an individual may have moved from their previous location and lost track of prey). For more detail, see equation A7 in appendices.

5.3.3 Capturing prey

Upon encountering prey, an individual will receive a fitness payoff if they are successful in capturing prey. The probability of successful capture p_0 is:

$$p_0 = \frac{ec}{\sqrt{g}} \quad (4)$$

Where e is the base probability of capture. This takes into account an animal's ability to catch prey, the prey species ability to avoid capture, prey distribution etc. Larger group sizes are assumed to be a hindrance due to increased competition and interference while underwater, reducing the probability of capture. Adverse conditions are also assumed to reduce the probability of capture.

5.3.4 Oxygen depletion and resting

All dive events result in increased oxygen depletion, the level of which depended on if an animal was below their aerobic threshold x_1 , at which point they were assumed to be diving anaerobically. Anaerobic dives result in greater

oxygen depletion than aerobic dives. If an individual chooses to rest, it reduces its oxygen depletion depending on if it has been diving anaerobically or not, with individuals below the aerobic threshold recovering slightly more quickly than those above. If diving would push the individual over the anaerobic threshold x_2 they are forced to rest. An individual must often choose between diving anaerobically in order to take advantage of current information and resting.

Table 5.3: Values of physiological parameters that control dive costs, recovery rates and aerobic and anaerobic thresholds.

Variable	Description	Value
x_1	Aerobic threshold	1.2
x_2	Anaerobic threshold	100
a_1	Aerobic diving cost	0.11
a_2	Anaerobic diving cost	2
b_1	Aerobic recovery rate	0.4
b_2	Anaerobic recovery rate	0.7

5.3.5 Computation

All models were written and run in Matlab. Physiological parameters were fixed at baseline values, based on the parameters used by Ydenberg and Clark (1989b), normalised so that anaerobic limit x_2 was 100 (Table 5.3). We explored the strategies (a rule for choosing between the actions available based on the animal's current state) that would maximise an individual's prey intake at T in differing conditions. A selection of different predator/prey interactions were considered, varying in the difficulty of finding and catching prey (see Table 5.4), and an animal's ability to judge the foraging success of conspecifics (see Table 5.5). For each of these, models were run for the full range of conditions (see Table 5.2) and for number of neighbours ranging from 0 (a solitary bird) to 10.

For each set of parameters, after initial calculation of values backwards iteration was used to solve for optimal strategy. To understand the implications for expected behaviour we calculated the likelihood that individuals following the optimal diving strategy would be of a particular state (and thus the probability of behaving in a particular way) at each timestep after starting with the initial states of no oxygen debt and having not encountered prey. Results are expressed as proportion of time spent carrying out a particular action.

Table 5.4: Predator/prey interactions and the values of associated variables: base probability of encountering prey l , base probability of maintaining contact with prey r and base probability of capturing prey e .

ID	Description	l	r	e
1	Prey easy to find, easy to maintain contact with and easy to catch.	0.5	0.8	0.8
2	Prey easy to find, easy to maintain contact with and hard to catch	0.5	0.8	0.2
3	Prey easy to find, hard to maintain contact with and hard to catch	0.5	0.6	0.2
4	Prey hard to find, hard to maintain contact with and hard to catch	0.2	0.6	0.2
5	Prey hard to find, easy to maintain contact with and easy to catch	0.2	0.8	0.8
6	Prey hard to find, easy to maintain contact with and hard to catch	0.2	0.8	0.2
7	Prey easy to find, hard to maintain contact with and easy to catch	0.5	0.6	0.8

Table 5.5: Individuals ability to assess conspecific foraging success and the values of associated variables

Description	h_0	h
An individual picks a conspecific at random to copy	0.5	0.5
An individual can assess the foraging success of a conspecific	0.5	0.8

5.4 Results

5.4.1 General rules for optimal diving

After thorough exploration of the model results, several patterns emerge. Firstly, as found by Ydenberg and Clark (1989b) the diving strategies adopted by individuals will vary depending on the amount of time left and their encounter state. When time remaining is large it is beneficial for an individual to always maintain an aerobic state as it allows it to dive more frequently. However informed animals become more likely to dive anaerobically no matter their level of oxygen depletion as remaining time becomes smaller, with individuals diving opportunistically and continuously until contact with the prey is lost or it is physically impossible for them to dive any more. When prey has not been found, an individual is more likely to rest and reduce their oxygen depletion, so long as there is time remaining for them to forage. Even uninformed animals already in anaerobic states become more likely to decide to remain in this state and keep diving as time remaining decreases. When time remaining is smaller (generally when $T-t \approx 50$), conserving oxygen for future use is of little value and individuals will begin to dive anaerobically even more frequently, whether they have encountered prey or not. These general rules were true of all combinations of parameters (Fig. 5.1, 5.2).

5.4.2 Prevalence of dive copying behaviour

When an individual was uninformed, it was always the optimal decision to attempt to copy the dive behaviour of a conspecific, switching to making PI dives once they had encountered prey, so long as their information remained up to date. A general pattern within all prey types was that dive copying was more prevalent in poorer conditions and when neighbour density was lower (Fig 5.2). Thus, the prevalence of dive copying behaviour increased as prey became more difficult to encounter and reencounter (Fig. 5.1, 5.2). Better ability to judge foraging success of conspecifics also reduced the number of copied dives, depending on the prey type (Fig. 5.1, 5.2). Differences between prey types generally had negligible effects on the number of copied dives, though frequency of copied dives increased slightly when prey was harder to catch (Fig 5.1). Frequency of dive copying behaviour was also higher when prey was significantly easier to find again than to find initially (Fig 5.1), though this effect was reversed when in better conditions.

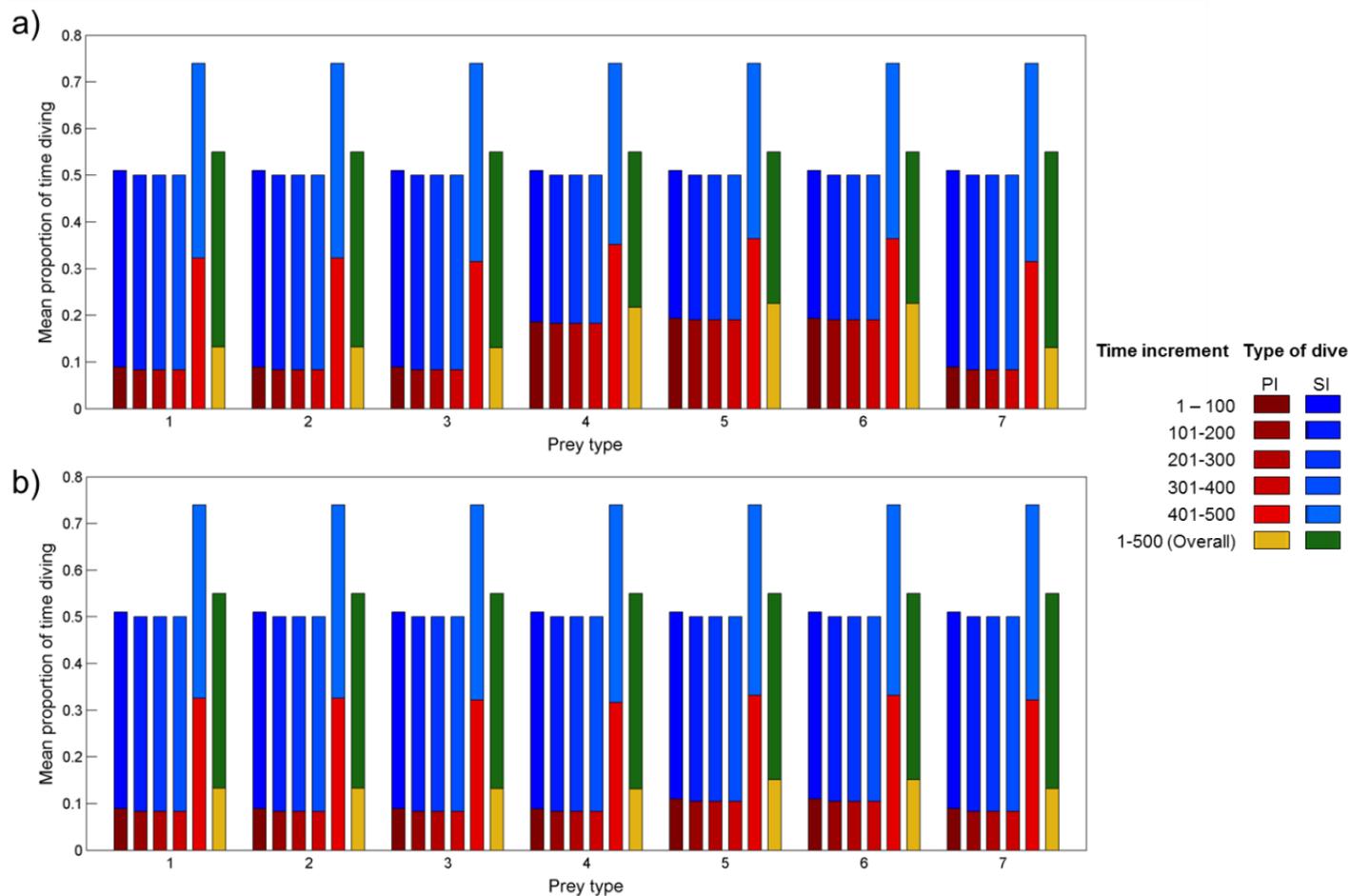


Figure 5.1: The results of the dynamic optimization model showing the proportion of time spent diving using personal information (PI) and diving using social information (SI) for differing prey types detailed in Table 5.4, for a) an individual with limited ability to judge conspecific foraging success and b) an individual with better ability to judge foraging success (see Table 5.5). The six bars for each combination of these two variables represent the results for each of five different time increments and for time overall (represented by differing colours, see legend).

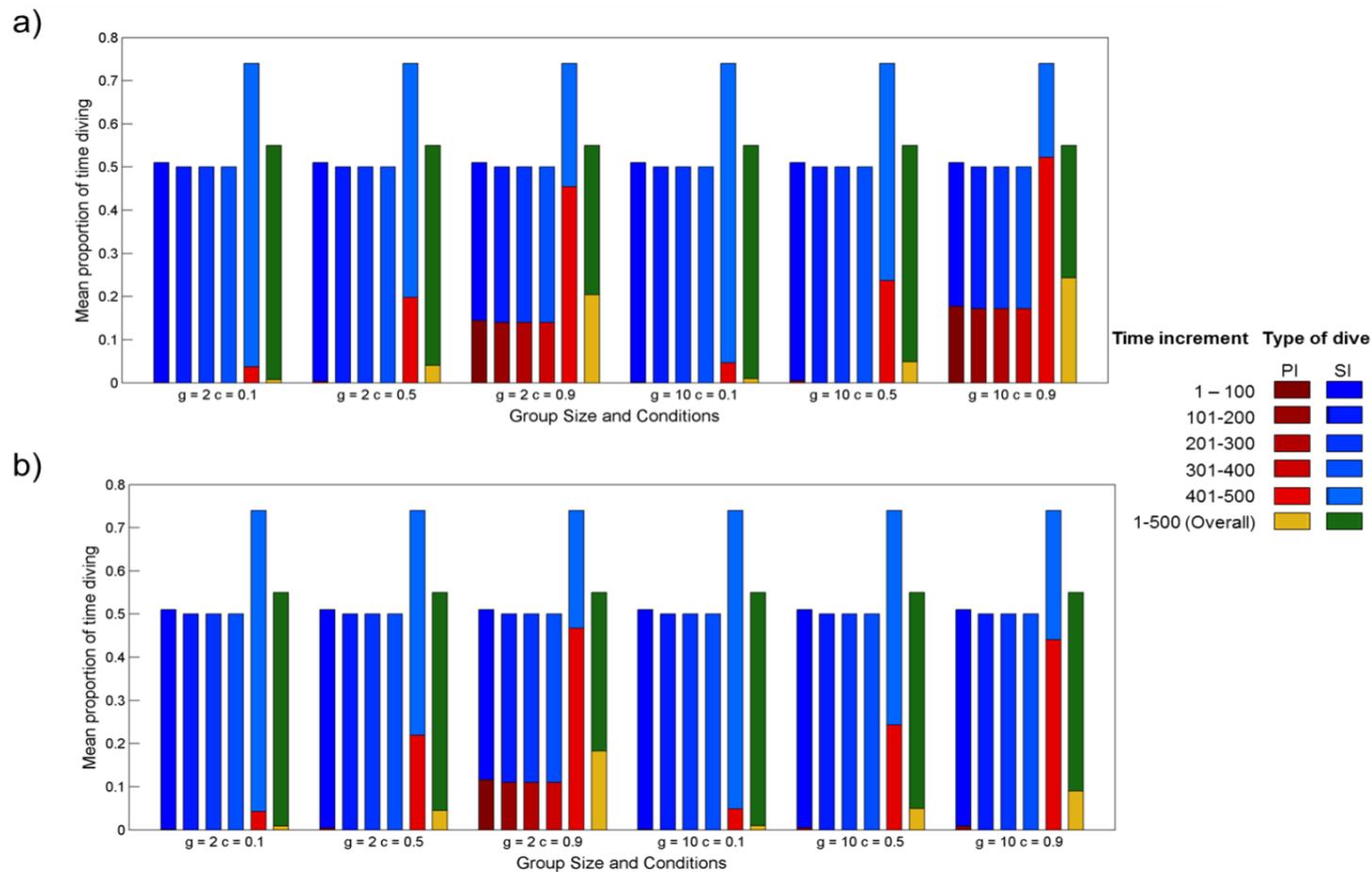


Figure 5.2: Further results of the dynamic optimization model, showing the proportion of time spent diving using personal information (PI) and diving using social information (SI) for different combinations of group size g and conditions c for a) an individual with limited ability to judge conspecific foraging success and b) an individual with better ability to judge foraging success (see Table 5.5). The six bars for each combination of these two variables represent the results for each of five different time increments and for time overall (represented by differing colours, see legend).

5.5 Discussion

The dynamic state model we describe here predicts the optimal decisions a diving animal will make depending on the nature of prey, group size, conditions and ability to judge the foraging success of conspecifics. The model suggests that, unless an animal has up to date personal information, copying the dive behaviour of a conspecific is always an optimal decision. We discuss these findings and their implications for understanding the ecological significance below.

Even when birds are unable to assess foraging success with any degree of accuracy, dive copying behaviour is still prevalent. In fact our model suggests that when animals can judge the foraging success of neighbours they are more likely to use those neighbours as indicators of prey on the surface than attempt to simply copy their dive behaviour. It seems likely animals will both copy the dive behaviour of conspecifics and use neighbours to keep track of the location of local patches of prey and that the synchronicity of dives may be affected by an inability to judge the exact foraging success of an individual. Dive copying behaviour, while extremely common in all parameter sets, became more common in poorer environmental conditions. This is likely due to the fact that information about prey location becomes out of date quite quickly in these conditions meaning that there is not much opportunity to make an informed personal dive. In addition, due to the difficulty of encountering prey, individuals are less likely to gain information about prey location. In these cases attempting to copy a more informed neighbour is does not present much risk. If the individual chosen is more informed, there is a higher probability of encountering prey. If the individual chosen is uninformed, then the probability of encountering prey is the same as it would be if the animal dived using their own personal information. The frequency at which dive copying occurs is therefore affected by an animal's

ability to collect personal information, and how long that information remains up to date. Good conditions and additional group members aid individuals in keeping track of prey, increasing the amount of time which their personal information is useful. In an empirical scenario, we may therefore expect to see a high degree of dive copying when visibility is low (thus preventing animals from retaining contact with prey for very long while on the surface) or in poor sea states or high tidal flows (where information rapidly becomes outdated and it is difficult to find prey in the first place).

According to the model, the prey type that will consistently lead to a greater degree of dive copying depended on the conditions. When conditions were good and the value of personal information was high (i.e, it was significantly easier to find prey having already found it), dive copying behaviour was significantly reduced.

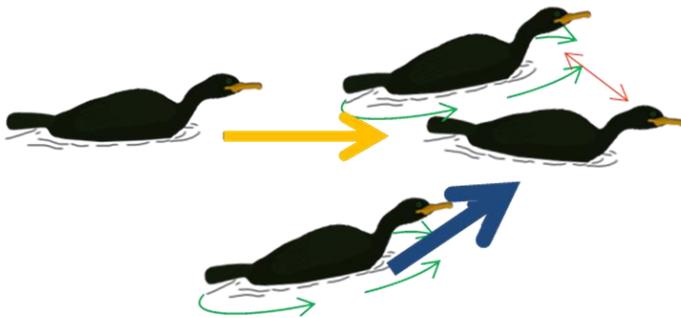
Individuals are able to make multiple informed dives, thus reducing the need to attempt to copy conspecifics. In poor conditions however, this effect was reversed. In this case while personal information was still valuable, an animal could not retain this information for very long. Attempting to find an informed conspecific could still lead to a higher payoff than attempting a naïve dive however, with no great loss if an uninformed conspecific was chosen.

While this is a complex model it still has some flaws in terms of biological realism, as the ratio of diving to resting behaviour seen in the model differs somewhat from empirical studies. Most glaringly, it focuses on a single individual within a group while abstracting the behaviour of other group members. When an individual chooses an informed conspecific, that conspecific is assumed to have encountered prey in the previous timestep. Similarly the model does not deal with neighbours playing different strategies. Developing this model into dynamic behavioural game would allow the behaviours and states of other group members to

be taken into account more accurately (Mangel & Clark, 1989). Much diving behaviour was focused towards the end of each foraging period ($t = 401 - 500$), with animals waiting till the end then continuously making dives or copying the dives of their conspecifics (Fig. 5.1, 5.2). This result is likely partly due to the assumption made that prey is abundant enough that it does not get depleted, even when the number of birds foraging increases. There is also no disadvantage to accumulating a large oxygen debt in the final timesteps due to the cut-off point. Likewise, there is no variation in time spent underwater or cost of diving. A future model should possibly model prey abundance and the speed at which it is depleted as function of time and number of neighbours, as this would be a more realistic interpretation of social diving.

In conclusion, our model demonstrates that copying the diving behaviour of neighbours can be a viable strategy, even when essentially choosing individuals at random. These results also suggest that the frequency of this behaviour will depend on how long personal information remains accurate. While this lends weight to the idea that availability of social information is an advantage of diving in groups, this must be tested empirically by studying the diving behaviour of individuals within groups. If individuals do use the diving behaviour of conspecifics to inform their own diving, we would expect to see individuals diving in close proximity to each other in time and space. This would require detailed datasets of the movements and diving behaviours of individuals diving in groups. High resolution GPS tracking of individual within a group, or video analysis of groups might provide an ideal way to test these ideas empirically. These methods would greatly help in exploring our suggestion that availability of social information is one of the main drivers of group foraging behaviour in aquatic air-breathers.

6. Inferring individual rules from collective diving behaviour



6.1 Abstract

Air-breathing animals that dive for food face enormous challenges - the constraint of locating and catching prey is compounded by the need to hold their breath. Most theoretical and empirical studies of foraging by diving animals focus on the physiological requirements of a single animal required to maximise prey intake. However, many species dive in large groups, but social diving behaviour has received little attention. Benefits from group diving include access to social information and reduced predation risk. However, these must be balanced against the costs of conspicuousness to predators or kleptoparasites, as well as competition and interference. Here we examine social diving behaviour for rafts of European Shags (*Phalacrocorax aristotelis*). Using video footage, we utilised group motion analysis to extract positions and trajectories of individual birds and fitted these data to zonal interaction models in order to examine the movement and diving rules of individuals. Individuals within the rafts moved in close proximity to each other and dives were heavily clustered in time and space. The best fitting models allowed individuals to use social information from neighbours when moving and deciding when and where to dive. These results suggest that individuals can use the dives of conspecifics when deciding when to dive themselves, which may be one of the main advantages of social diving.

6.2 Introduction

Numerous air breathing animals dive to find food underwater. During this time animals are under physiological pressure, balancing their need to capture prey with their requirement to return to the surface and breathe (Houston & Carbone, 1992; Kramer, 1988). In order to maximise foraging efficiency they must constantly make decisions about when, where, how deep and how often to dive, as well as how long

to remain submerged (Heithaus & Frid, 2003; Houston & Carbone, 1992; Mori, 1998; Regular, Hedd & Montevecchi, 2013; Sparling *et al.*, 2007). Multiple studies, both empirical and theoretical, have investigated how these decisions affect an animal's ability to remain underwater and forage efficiently (Brandt, 1984; Heaslip, Bowen & Iverson, 2014; Mori, 2002). However, most of these studies examine the diving behaviours of single animals while many air-breathers, especially seabirds, dive in groups (Battley *et al.*, 2003; Beauchamp, 1992; Brandt, 1984).

Animals may dive in groups simply because of aggregated prey. Under these circumstances individuals may be expected to form large chaotic groups with much intraspecific competition (Barnard *et al.*, 1982; Battley *et al.*, 2003; Hoffman *et al.*, 1981). However, many group diving animals display a high degree of alignment and polarity (Beauchamp, 1992; Berlincourt & Arnould, 2014; Schenkeveld & Ydenberg, 1985b; Takahashi *et al.*, 2004a). Such coordination, combined with the high synchronicity of diving displayed in these groups is likely driven by benefits other than those derived simply from aggregating. These advantages must also outweigh the increased competition (Foster, 1985; Ranta *et al.*, 1993), kleptoparasitism (Ranta *et al.*, 1993), predation (Cresswell, 1994) and interference (Ruxton, 1995) animals suffer when diving in groups.

Possible benefits of diving in groups may include reduced individual risk (Roberts, 1996), enhanced predator detection (Beauchamp, 2001; Cresswell, 1994), resource access (Dall & Wright, 2009a) or foraging efficiency. There are a number of ways social diving might improve foraging efficiency. Animals could gain hydrodynamic benefits by diving together, reducing energetic costs (Noren *et al.*, 2006). Groups may even engage in semi-cooperative prey herding behaviour, forcing prey into areas where they can be more easily exploited (Battley *et al.*, 2003;

Benoit-Bird & Au, 2009). Improved foraging efficiency might also be achieved by utilising social information from conspecifics to reduce uncertainty (Dermody *et al.*, 2011; Templeton & Giraldeau, 1995), which is particularly relevant given the time and energetic requirements of diving (Enstipp *et al.*, 2007; Williams *et al.*, 2000; Williams & Yeates, 2004; Wilson *et al.*, 1992). Animals on the surface can reduce uncertainty by utilising the location, diving and resurfacing behaviour of their conspecifics within the group as indicators of the distribution of localised prey patches underwater. This could also allow animals to keep track of underwater prey while resting on the surface (Stempniewicz *et al.*, 2013; White *et al.*, 2007). Furthermore, individuals may benefit from simply copying the diving behaviour of their conspecifics, diving synchronously to capitalise on short term changes in food availability (Brumm & Teschke, 2012; Schenkeveld & Ydenberg, 1985a). Animals that dive collectively would likely use all these tactics, and we therefore may expect individuals to not only copy when their conspecifics dive but also where they dive.

Here we explore the mechanisms of group diving in large flocks of European shags (*Phalacrocorax aristotelis*) to look for evidence of social information use while diving. European shags (hereafter shags) are colonial breeding, pursuit diving seabirds. They forage in sandy, rocky areas at depths of up to 40 metres, mainly on small fish such as sand eels, which they swallow underwater (Nelson, 2005). Shags frequently engage in group diving behaviour, forming large flocks (hereafter referred to as “foraging rafts”) while foraging. These foraging rafts consist of several hundred birds moving along the surface of the water and diving together, displaying a high degree of cohesion and alignment. Similar formations can also be found across a wide range of marine birds, including; surf scoter (*Melanitta perspicillata*) (Lukeman *et al.*, 2010b), Barrow’s goldeneye (*Bucephala islandica*) (Schenkeveld and

Ydenberg 1985; Beauchamp 1992), American White Pelican (*Pelecanus erythrorhynchos*) (Anderson 1991) and numerous Phalacrocorax species (Nelson, 2005). These differ from non-foraging aggregations such as the compass rafts of Guanay cormorants *P. bougainvillii* (Weimerskirch, Bertrand et al. 2010), seabird rafts near colonies (Wilson, McSorley et al. 2009) or waterfowl flocks for anti-predator reasons (Fox, Green et al. 1994; Fox and Mitchell 1997).

Rafting was studied using video analysis. Other approaches such as bio-logging and individual marks are not currently tractable, whereas advancements in video analysis and automated tracking software now allow the positions and trajectories of individuals to be extracted from images of animal groups. This has allowed the analysis of aggregations under natural conditions and their reactions to external stimuli such as predators or kleptoparasites (Ballerini *et al.*, 2008b; Buhl, Sword & Simpson, 2012; Capello *et al.*, 2011). The use of these techniques, accompanied by increases in available computing power has allowed the development of numerous models of collective behaviour. Both controlled laboratory experiments (Berdahl *et al.*, 2013; Ioannou, Guttal & Couzin, 2012) and field studies (Ballerini *et al.*, 2008a; Cavagna *et al.*, 2010; Lukeman *et al.*, 2010b) have shown how simple behavioural rules can lead to complicated group behaviours. These techniques have been effective in the study of flocking in birds (Ballerini *et al.*, 2008a; Schenkeveld & Ydenberg, 1985a) and schooling fish (Katz *et al.*, 2011), but have not been used for studying group diving.

Here we utilise techniques for examining the collective motion of two dimensional bird flocks (Lukeman *et al.*, 2010b). Specifically we analyse individual surface movements by comparing empirical data with the results of individual-based simulations. We also examine surface movement in relation to social diving, to

understand how individuals might alter their own behaviour in relation to others. If birds are using social information to inform dive decisions we predict a high degree of following and attraction toward dive or resurface events.

6.3 Methods

6.3.1 Data collection

Video data were collected in the Isles of Scilly (49.9361° N, 6.3228° W, UK), from a vantage point on the island of St. Martin's in June and July 2013, avoiding adverse weather conditions. This location was selected based on a previous research showing that rafts of shags frequently foraged in this location (See **Chapter four**). Footage was captured using a video camera (Sony Handycam HDR-CX190E, Tokyo, Japan) at 25 frames per second at a resolution of 1920 × 1080 pixels. During the filming of each sequence the camera position, heading (in relation to magnetic north), angle and elevation (height of tripod added to the height of terrain at the observation point) were locked and recorded. The lower edge of the image was always aligned with the nearest shoreline. Upon sighting, rafts were filmed continuously until there were no birds left in frame.

6.3.2 Video processing and position extraction

Videos were analysed frame by frame using Matlab (MATLAB, 2014). Birds were extracted from the background using image processing tools (Fig. 6.1B). Each frame was averaged using a selection of the proceeding and successive frames in order to avoid erroneously extracting light flickering on the water (the number of frames each individual frame was averaged over was set dependant on the video). Image processing functions (including `rgb2gray`, `im2double`, `imadjust`, and

regionprops) were used to convert each frame into a black and white image, with shags appearing in black (Fig. 6.1B). Statistics and centroid coordinates were extracted for each individual shape present in the image (Fig. 6.1A). These shapes were then filtered based on their areas, with shapes that were too small or too large to be birds discarded (area varied between sequences, average body size was 20 pixels). Remaining shapes' centroid coordinates were then recorded.

Horizontal and vertical transformations were used to transform coordinates so as to correct for any perspective distortion introduced by the camera or the oblique angle at which we filmed (Lukeman *et al.*, 2010b).

The actual distance y of points from the shore aligned with the bottom of the frame (in pixels) were obtained after first calculating the angle of view of the camera ϕ and the camera axis angle for that particular sequence θ (See **Appendix 6.1**). The range $0 \leq \hat{\phi} \leq \phi$ (where $\hat{\phi}$ is the angle corresponding to y) was then mapped linearly onto the image's vertical pixel range [0, 1080]. Any value of y can be then be found by:

$$y = \frac{1080}{\phi} \left(\tan \left(\theta + \frac{p\phi}{1080} \right) - \tan(\theta) \right)$$

Where the vertical pixel p is:

$$p = \frac{1080\hat{\phi}}{\phi}$$

For horizontal transformations we photographed a two known lengths with a camera angled at mean θ (79.46). The ratio between the actual lengths (top edge)/(bottom

edge) of this image, which gave the maximum perspective distortion was then used to correct for any horizontal perspective distortion (Lukeman *et al.*, 2010a).

Corrected positions from each frame were connected to create trajectories (Fig. 6.1C). The algorithm used predicts positions based on estimated position and velocities using linear quadratic estimation, and then calculates the distances between observations and predictions. The optimal trajectory to place an observed position was then selected based on an auction algorithm (Bertsekas, 1991).

Trajectories where birds appeared to be moving unrealistically fast or slow were removed (velocities of greater than 2.5 body lengths per second or less than 0.2 body lengths per second). Trajectories were checked for accuracy by reviewing back-transformed corrected positions on the original footage (Fig. 6.1D). Custom functions were then used to merge and refine trajectories and delete erroneous fixes. As with Lukeman *et al.* (2010a), individuals on the leading edge of the flock were excluded from analysis. Individuals on the edge of groups will experience different hydrodynamic and environmental conditions to those in the centre of the group, as well as potentially affecting the decisions of other members through leadership effect.

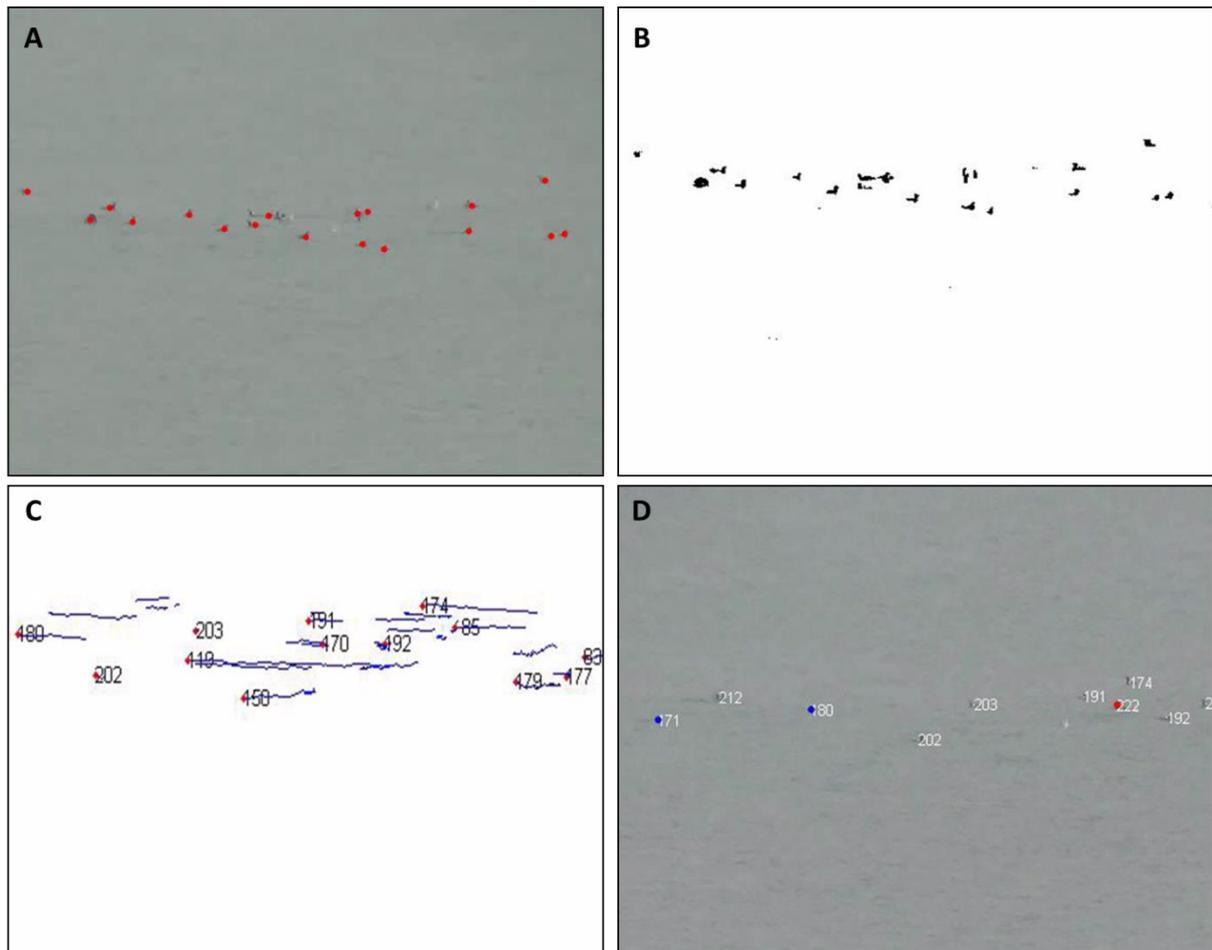


Figure 6.1: Example of video analysis process, A: Raw image with centroids, B: Image processed to extract individuals from background, C: Trajectories of individuals after correction for camera height, field of view etc. (See supplementary info of Lukeman, Li et al. (2010b)), D: Corrected positions, detected dives (blue) and detected resurfaces (red) back transformed onto original video so as to ascertain tracking accuracy.

Diving and resurfacing activity was detected using a custom script. When detecting dives the script checked that a trajectory that ended within a bounding-box 10 pixels smaller than the frame met certain criteria. One of the main criteria was an increase in area (due to the slight splash produced) followed by a rapid decrease in area over the course of two seconds. Trajectories that began in this bounding box were detected as resurfacing events. Relative neighbour positions were calculated for each (non-edge) individual in each frame in each sequence. These were

averaged together to produce a 2d plot of the entire dataset, giving the probability of a neighbour being at relative position. This density plot was normalised so that the highest density was 1 (Fig. 6.2a). Similar plots were created for the relative position of dive and resurface events (Fig. 6.2). Bin size in both these plots was 1 body length \times 1 body length (BL) . The relative alignment of neighbour's for the entire dataset, consisting of the differences in heading between a focal individual and their neighbours, were sorted into bins of 10° and plotted to create a 1 dimensional histogram of density of relative neighbour alignment (Fig. 6.2b). Synchronicity was assessed by recording the intervals between sequences successive dive or resurface events, with the expectation that synchronous diving would produce more short than long intervals (Schenkeveld & Ydenberg, 1985b). These intervals were plotted on another 1 dimensional histogram.

6.3.3 Simulation and comparison with empirical data

The collated data were compared to statistics extracted from simulations based on a hierarchy of individual-based zonal models (Couzin *et al.*, 2002; Lukeman *et al.*, 2010b). All simulations were written and run in Matlab and consisted of three main components: (1) the movement of birds on the surface, (2) the diving/resurfacing of birds and (3) the interaction between these.

Model of surface movements

The model used to govern the position x and velocity v of an individual i is:

$$\begin{aligned} \vec{x}_i &= \vec{v}_i \\ \vec{v}_i &= \vec{f}_{i,aut} + \vec{f}_{i,int} + \vec{f}_{i,dint} + \vec{f}_{i,rsint} + \vec{\xi}_i \end{aligned}$$

Where $f_{i,int}$ represents the interactions with neighbours, $f_{i,aut}$ the autonomous movement of an individual, $f_{i,dint}$ the interaction with diving events, $f_{i,rsint}$ the interaction with surface events and ξ_i is Gaussian noise. These interaction forces were our main focus as we are primarily interested in how individuals interact and use social information from conspecifics within the raft. Birds on the surface make a series of decisions based on the distribution of neighbours within concentric zones of interactions (Fig. 6.3, Table 6.1). The contribution of individual neighbours is distance weighted so that nearer neighbours will have a greater influence on movement than those further away (For more detail see Lukeman, Li et al (2010b)). The radii of zones were estimated from the data (Fig 6.2).

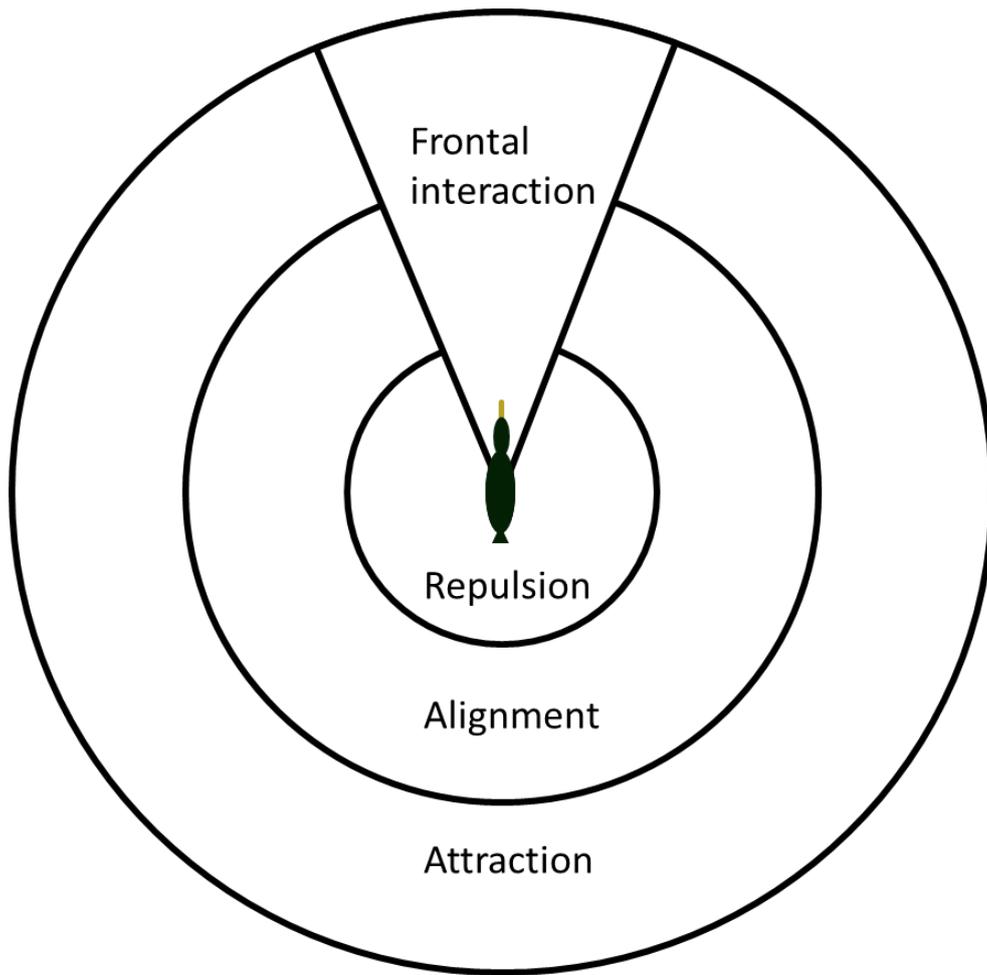


Figure 6.3: Illustration of the four zones of interaction surrounding a simulated focal individual, which are used when making movement decisions (Table 6.1).

Table 6.1: Descriptions of the movement rules an individual utilises, depending on the location of neighbours within concentric zones of interaction (Fig. 6.3).

Zone of interaction	Description of movement rule followed
Zone of repulsion	An individual will accelerate away from the distance-weighted average of neighbours within this zone.
Zone of Alignment	An individual will attempt align itself with neighbours within this zone.
Zone of attraction	An individual will move towards to the average position of neighbours within this zone.
Zone of frontal interaction	A zone consisting of an angular section with angle 60° within the zone of attraction. Individuals will have an attraction/repulsion interaction with a single nearest neighbour within this zone.

As with Lukeman, Li et al. (2010b) we modelled these forces as normalised piecewise linear pairwise interaction forces, the magnitude of which could be controlled using weighting parameters ω_k (where k is the type of force, e.g attraction to dives, attraction to neighbours etc.) in order to experiment with different ways that neighbours might cause changes in movement use. These parameters can be altered to test different model types and optimised using a goodness of fit measure detailed below.

$$\vec{f}_{i,int} = \omega_{rep} \vec{f}_{i,rep} + \omega_{al} \vec{f}_{i,al} + \omega_{att} \vec{f}_{i,att} + \omega_{front} \vec{f}_{i,front}$$

Interactions with dive/resurface events

As well as autonomous movement and interaction with neighbours a bird's movement was also affected by interaction with dive events and interaction with surface events.

$$\vec{f}_{i,dint} = \omega_{drep} \vec{f}_{i,drep} + \omega_{dal} \vec{f}_{i,datt}$$

$$\vec{f}_{i,rsint} = \omega_{rsrep} \vec{f}_{i,rsrep} + \omega_{rsal} \vec{f}_{i,rsatt}$$

As with interactions with neighbours on the surface, these interactions are modelled as decisions based on the location of dive and resurface events within zones of interaction and are given appropriate weighting parameters so as to investigate differing models. Thus, birds can be attracted to or repulsed from dive and resurface events. Diving and resurfacing events were simulated based on a combination of predefined diving and surfacing rules (Table 6.2, Table 6.3). In all resurfacing rules simulated birds stay underwater for a minimum time of five seconds after diving (the shortest recorded dives from observation of solitary shags diving). After this the probability of resurfacing increases every frame.

Table 6.2: Description of the three different ways in which diving decisions were simulated.

Dive rule	Description of diving rules followed
D1.	Simulated birds dive randomly. No social information use.
D2.	Simulated birds are more likely to dive when another simulated bird dived or surfaced recently depending on their proximity in space and time (within 2 seconds). Birds responding to the same underwater stimuli, no social information use.
D3.	As with D2, but simulated birds have a limited field of view, only detecting dives that happen within a 60° arc ahead of them (White <i>et al.</i> , 2007). Birds utilise their conspecifics as sources of social information.

Table 6.3: Description of the three different way resurfacing behaviour was simulated.

Resurface rule	Description of resurfacing rules followed
RS1.	Birds resurface within a circle of random radius centred on the location of their dive, with a maximum radius depending on how long a bird was underwater. No social information use underwater.
RS2.	As with RS1, but simulated birds are more likely to resurface closer to another simulated bird. When resurfacing, the bird has a higher probability of surfacing within the flock. No social information use underwater.
RS3.	This rule attempts to simulate the effects of birds following each other underwater. Similar to 2, however a “following” bird is more likely to resurface in close proximity (in time and space) to a “leading” bird it dived in close proximity to (in time and space). When a “leading” bird resurfaces, the probability of the “following” bird surfacing is increased. The “following” bird has a higher probability of surfacing near the “leading” bird. Birds using conspecifics as sources of social information use underwater.

6.3.4 Goodness of Fit Measure and optimisation of parameters

To establish the relative importance of interaction forces (and thus establish how much influence conspecific neighbours might have on an individual’s movement diving behaviour) we carried out parameter optimisation on these weighting parameters, attempting to match simulation results to the positions extracted from video data. Simulation results were compared to empirical data using the sum of

three goodness-of-fit measurements, which in turn each consisted of the sum of two different error types.

Firstly, as with Lukeman, Li et al. (2010b) we compared the relative position and alignment of neighbours moving on the surface of the water using the sum of the mean-squared difference between recorded and simulated relative 2d neighbour densities and relative alignment.

$$mE = \langle (\rho_{data}(x, y) - \rho_{sim}(x, y))^2 \rangle + \langle (h_{data}(\theta) - h_{sim}(\theta))^2 \rangle$$

Where $\langle \cdot \rangle$ is a mean, ρ is the relative 2D spatial distributions of neighbours, and h is the relative alignment of neighbours. The other goodness of fit measurements test the simulations accuracy at predicting the time and location of diving and resurfacing:

$$dE = \langle (d\rho_{data}(x, y) - d\rho_{sim}(x, y))^2 \rangle + \langle (d\kappa_{data}(s) - d\kappa_{sim}(s))^2 \rangle$$

$$rsE = \langle (rs\rho_{data}(x, y) - rs\rho_{sim}(x, y))^2 \rangle + \langle (rs\kappa_{data}(s) - rs\kappa_{sim}(s))^2 \rangle$$

Where ρ is the 2D spatial distributions of dive/resurface events relative to other events (i.e. how close these events were to each other in space) and κ is the interval between events in seconds (i.e. how close there events were to each other in time (Schenkeveld & Ydenberg, 1985a)). These three measures were summed to produce an overall goodness of fit measure, E (though the contributions of all three were considered and reported when comparing models).

$$E = mE + dE + rsE$$

Initially all parameters were explored manually in order to establish initial ranges. E was then refined using Matlab's built-in optimisation algorithm "fmincon", which attempts to minimise a functions' output within specified constraints. The ranges derived from the manual exploration were used as constraints. Each set of weighting parameters was run with all combination of dive/resurface rules and simulations were run 20 times for each set of parameters/rules. After optimisation the best fitting model was compared to models representing varying levels of information use and a null model consisting where individuals moved and dived completely randomly (Table 6.4).

6.4 Results

6.4.1 Analysis of Empirical data of group diving behaviour

Analysis of video data revealed that while on the surface, mean nearest neighbour distance was 6 ± 4 SD body-lengths (Fig. 6.2a) and birds travelled at a mean speed of 1.1 ± 1 SD BL/s. Neighbours in front of individuals tended to be closer than those behind, and in general, at larger distances $> \approx 15$ BL, more neighbours were focused behind and in front than to the left or right. Movement was highly polarised with most individuals moving in similar directions (Fig. 6.2b). Dives were also heavily concentrated within a few body lengths of each other and appeared to be primarily focused just behind focal dives (Fig. 6.2c). Dives showed clear synchronicity with many dives taking place within two seconds of each other (Fig. 6.2d) Resurfacing events were also fairly clustered in space and time, though to a lesser extent (Fig. 6.2e and Fig. 6.2f).

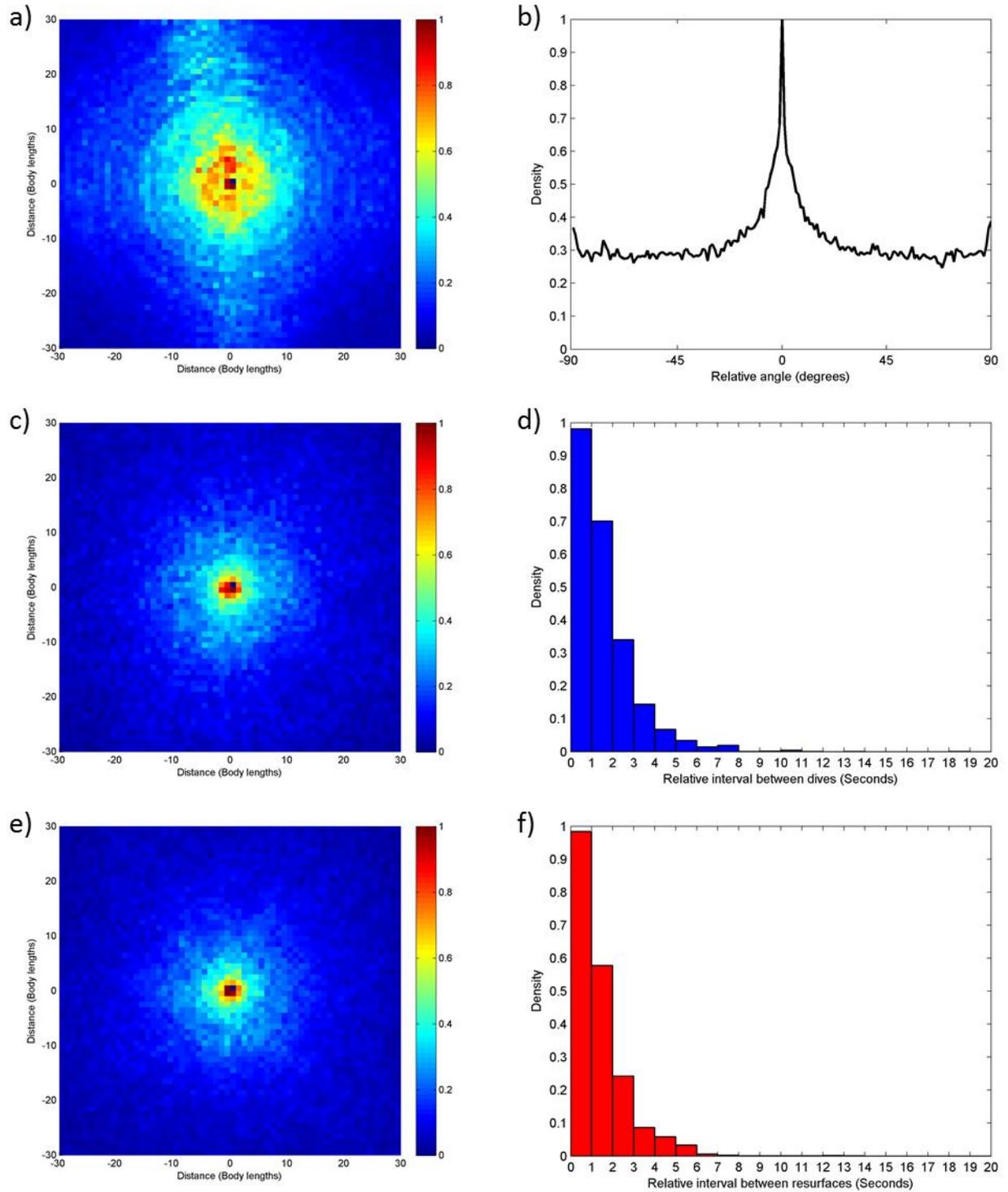


Figure 6.2: Results from empirical data on diving behaviour: a) Density of relative neighbour positions, b) Density of relative neighbour alignment, c) Density of dive events relative to other dive events, d) Synchronicity of dive events, e) Density of resurface events relative to other resurface events, f) Synchronicity of resurface events.

6.4.2 Comparisons with simulations of group diving behaviour

The chosen top model fitted the data considerably better than any null models (Table 6.4). These included a purely random walk (which we might expect in a chaotic assemblage), a simple model of attraction and repulsion (simulating basic collision avoidance while maintaining some cohesion), models not taking dives or resurface events into account (which would be the case if diving and resurfacing generated no social information about the location of prey, but does not preclude conspecifics copying the timing of dives), models only taking dives into account (which would suggest that resurface events are not a useful indicator of prey location or availability) and a model in which all forces were weighted equally (which would suggest that the position of conspecifics on the surface are taken into account, but no one force dominates).

Table 6.4: The model that was found to best fit empirical data, contrasted with a selection of null models. Each model is presented with its total error E and the three differing types of error used to calculate E .

ω_{rep}	ω_{att}	ω_{al}	ω_{Fint}	ω_{Drep}	ω_{Datt}	ω_{RSrep}	ω_{RSatt}	D rule	RS rule	E	mE	dE	rsE
97	96	12	83	34	81	20	76	D3	RS2	0.02	0.01	0.007	0.004
0	0	0	0	0	0	0	0	D1	RS1	0.09	0.06	0.016	0.015
100	100	0	0	0	0	0	0	D1	RS1	0.11	0.07	0.014	0.021
25	25	25	25	0	0	0	0	D2	RS2	0.09	0.07	0.010	0.008
25	25	25	25	25	25	0	0	D3	RS2	0.07	0.05	0.008	0.006
25	25	25	25	25	25	25	25	D3	D2	0.07	0.05	0.007	0.009

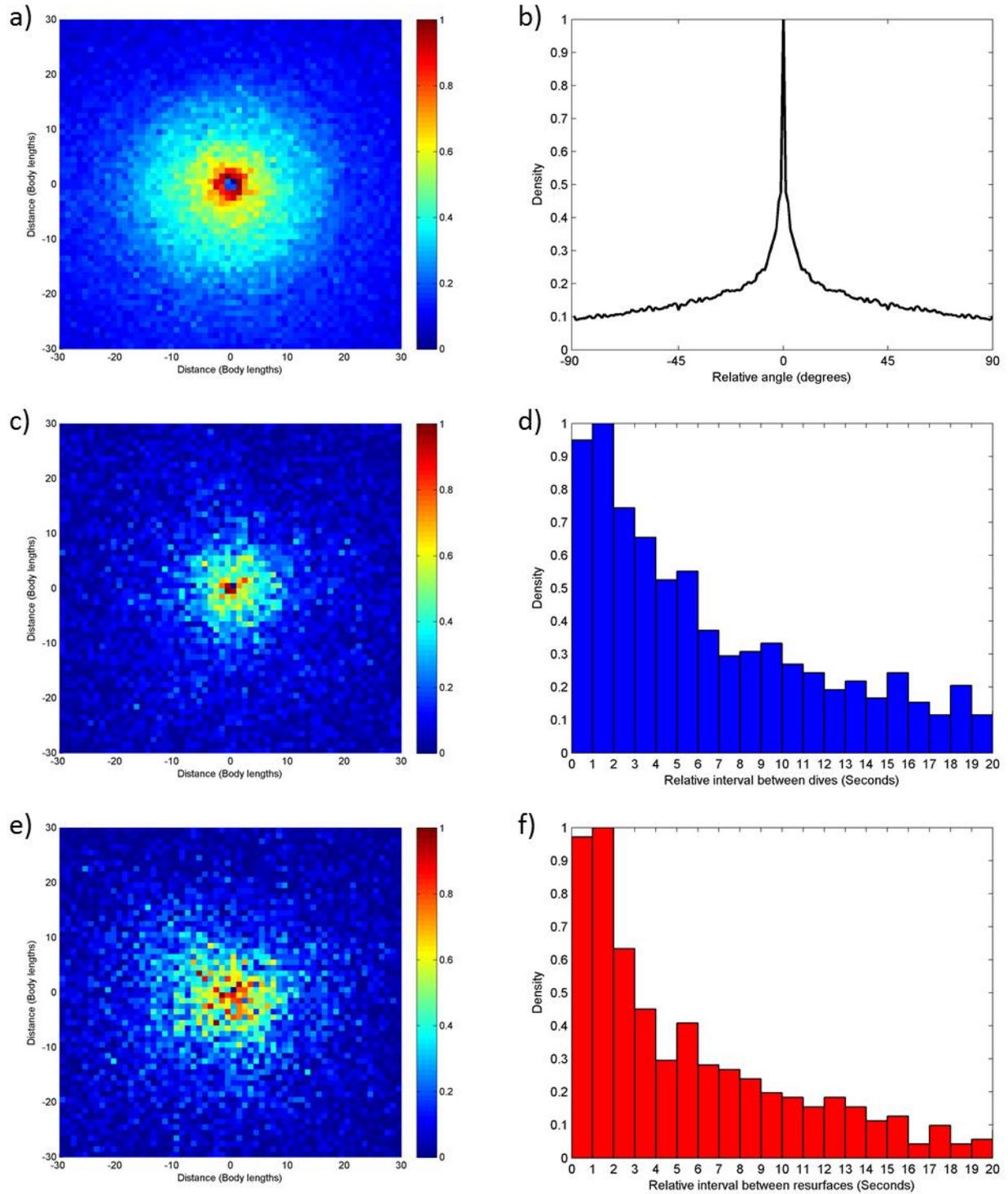


Figure 6.4: Results of best fitting model (Table 6.4, Figure 6.5). a) Density of relative neighbour positions, b) Density of relative neighbour alignment, c) Density of dive events relative to other dive events, d) Synchronicity of dive events, e) Density of resurface events relative to other resurface events, f) Synchronicity of resurface events.

This model displayed strong forces of repulsion, attraction and frontal interaction but extremely weak alignment forces (Fig. 6.5). Strong attraction was also shown towards dives, and a slightly weaker attraction towards resurfacing individuals (Fig. 6.5). Dive rule 3 and resurface rule 2 were found to give the most realistic results in terms of event location and synchronicity (Table 6.4). Despite this, simulations failed to display the extremely high degree of dive synchronicity observed in the empirical data (Fig. 6.4).

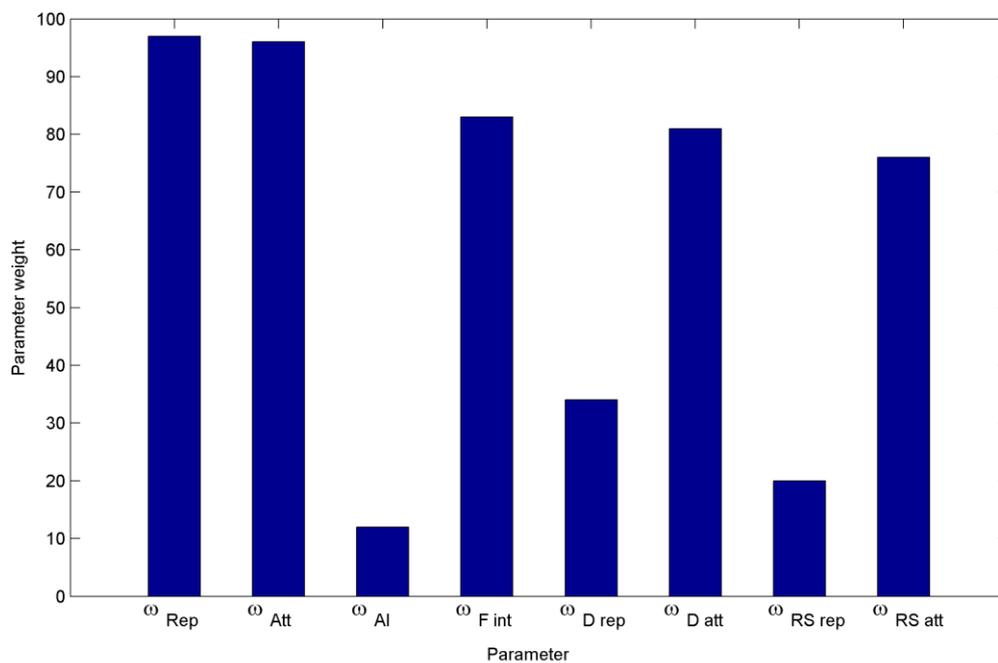


Figure 6.5: Magnitudes of forces of best fitting model (Table 6.4) as determined by the weighting parameter ω . Where Rep is repulsion, Att attraction, Al alignment, F int frontal interaction, D rep repulsion of dive events, D att attraction to dive events, RS rep repulsion from resurface events and RS att attraction toward resurfacing events.

6.5 Discussion

Here we present one of the first systematic studies of the behavioural rules governing group diving behaviour in an air-breather. We significantly advance a previous model of collective behaviour in birds (Lukeman *et al.*, 2010b) by incorporating a diving element. By comparing empirical video analysis results with simulations of collective motion with different rules of diving and resurfacing we take the first steps towards understanding this common and understudied behaviour.

6.5.1 Surface Interactions

Analysis of the relative spatial distribution of neighbours found a peak of density in front and behind each individual, (Fig 6.2a). This, along with our simulations demonstrates that a high degree of following takes place within rafts. Following behaviour may aid in finding cryptic underwater prey or confer a hydrodynamic benefit. However a previous study of the conditions in which rafts form showed that rafting is less likely in faster tidal flows, during high tides, suggesting that foraging rafts do not allow individuals to counteract the disadvantages of foraging in these conditions, (See **Chapter four**). Forces of attraction among diving shags were also strong, indicating that birds actively move towards conspecifics. While this may be linked with anti-predation benefits, this seems doubtful due to the lack of natural predators of shags on the Isles of Scilly. There may be some benefits for diluting kleptoparasites as gulls were observed attacking shags, although such interactions were rare. It therefore seems more likely that birds are attracted to conspecifics because they provide an indication of prey distribution or because it might be beneficial to copy the areas neighbours are diving in (Galef Jr & Giraldeau, 2001).

Despite the high degree of polarity shown in rafts (Fig. 6.3b), alignment forces were found to be extremely weak in the selected top model (Fig. 6.5). These results are similar to previous studies of collective movement (Katz *et al.*, 2011), but differ from studies of two dimensional bird flocks, which found alignment forces to be more important than frontal interactions (Lukeman *et al.*, 2010b). These differences among studies are not well understood, but the relatively less dense and slower moving shags (when compared with diving ducks who had an average speed of 2 BL/s (Lukeman *et al.*, 2010b)), may allow the force of frontal interaction alone to confer similar relative alignments, suggesting that following behaviour might be the main driver of heading. Conversely, the extremely strong force of repulsion found with shags is consistent with other studies, which is likely due to the costs of failing to avoid collisions or aggressive interactions with conspecifics. Maintaining spacing while in the group might also allow more efficient diving or movement, and reduce the probability of collision on resurfacing.

6.5.2 Diving and resurfacing behaviour

Dives were tightly clustered in time and space, with a tendency for the closest dives to be slightly behind other dive events (Fig. 6.2c). The diving rule used in the best fitting model was one in which birds were more likely to dive if a conspecific within their field of vision had recently dived in close proximity (D3, Table 6.2). This proved a better predictor of dive behaviour than if individuals were simply reacting to the same stimuli underwater and diving based on their personal information, or completely random diving (Table 6.4). Likewise, birds in the most parsimonious model displayed a strong attraction towards the dives of conspecifics. Taken together these results strongly point towards a strategy where individuals observe and copy when and where conspecifics are diving. Diving or resurfacing

conspecifics might also be important for providing detailed information about underwater prey distribution underwater (Machovsky-Capuska *et al.*, 2012; White *et al.*, 2007). In this case it would be beneficial to dive close to diving or resurfacing conspecifics, even if it is difficult to assess conspecific foraging success, which is likely here as shags generally swallow their prey underwater (Rands *et al.*, 2003, see **Chapter five**). Diving in the same area as a conspecific may also be beneficial because prey might be flushed or fatigued by the previous individual (White, Butler *et al.* 2008).

The resurfacing rule in the chosen model allowed birds to surface at random times, but with increased likelihood of surfacing within the group. (RS2, Table 6.3). This may indicate that it is advantageous to attempt to remain within the raft due to group foraging benefits gained. Alternatively the tendency to resurface within the raft may simply be because shags do not travel very far while underwater. However, it seems unlikely that rafts are maintained purely due to short travel distances underwater, as this would likely result in rafts losing their long, thin formation and spreading out. The chosen top model appears to rule out direct following underwater (as simulated by RS3, Table 6.3). If birds use conspecifics dives as an indicator of local prey availability and copy when and where they dive there will likely be a short delay in some cases while the bird moves towards that dive. Similarly, a bird might choose to dive immediately upon observing a conspecific dive, due to the assumption that prey might be immediately available beneath the surface. In both these cases, attempting to then find the same conspecific underwater so as to follow them to a localised prey patch may be of little benefit, due to increased chance of competition and interference. This may be also be affected by the relatively shallow

depths at which shags dive in the islands (Nelson, 2005). Potentially, deeper diving species could benefit more from following conspecifics.

6.5.3 Further study and applications to other group divers

It would be beneficial to test some of these assumptions using similar techniques to other socially diving species, especially those that might feed in different environments and on different prey (Battley *et al.*, 2003; Beauchamp, 1992; Berlincourt & Arnould, 2014; Schenkeveld & Ydenberg, 1985b; Takahashi *et al.*, 2004a). This would aid in shedding light into the importance of information in similar systems, as well as the potential for following behaviour underwater. For example, we might expect our predictions to vary dramatically depending on prey type. Shags feed on highly motile prey, which likely has a significant influence on the patterns we observed. The different diving behaviours of animals that feed on sessile prey such as surf scoters might lead to differences in social information use within the group. Further studies might also choose to utilise more detailed simulations of movements underwater and methods of modelling collective behaviour. While models of zonal interaction were useful for predicting the movement of individuals, our models struggled to predict the same degree of synchronicity of diving and resurfacing observed in the empirical data (Fig. 6.2, Fig. 6.4). This may be due to the way in which underwater interactions were simulated, with the time spent and movements of individuals underwater abstracted and semi-random with no opportunity for submerged individuals to interact. Better understanding of behaviour while diving, possibly through the use of underwater cameras or acoustic imaging (Takahashi *et al.*, 2004b), might indicate the need for a more complex simulation of underwater interactions. Future work would also benefit from a more robust statistical framework

to investigate the exact influence conspecifics have on dive decisions (Delgado *et al.*, 2014).

6.5.4 Conclusions

In conclusion, our study provides the first steps towards deciphering the advantages and behavioural rules that govern social diving behaviour. Our results suggest that shags utilise the diving behaviour of conspecifics to inform personal dive decisions. This may be due to a combination of individuals using the surface movements and diving behaviours of neighbours as indicators of prey underwater and actively copying the decisions of their conspecifics. We propose that increased foraging efficiency due to the ability to obtain this social information from conspecifics may be one of the main advantages of choosing to dive in a group.

7. General Discussion



7.1 Overview

I have used a variety of methods to investigate group foraging behaviour and information use in a colonial seabird at several different scales. These methods included using GPS tracking techniques to carry out a broad examination of the foraging habits of individual European shags, followed by behavioural observations of the formation and movements of foraging rafts, and finally an investigation of the rules governing individuals within those rafts. The results of these studies show that while shags may not engage in information transfer at their home colonies, use of social information is highly likely while on prey patches. The studies also indicate that this easy availability of social information might be one of the primary benefits for individuals feeding in foraging rafts. While the times and places in which foraging rafts were observed was significantly affected by changes in sea state and tide, the exact conditions suggested that foraging rafts were unlikely to involve fish herding behaviour or bestow hydrodynamic advantages. Furthermore, analysis of the movement of individuals showed that individuals can use the dive behaviour of others to inform their own diving decisions. A state dependent dynamic optimisation model showed that this can be a useful tactic even when animals are unable to accurately judge the foraging success of others. By copying the diving behaviour of random conspecifics, individuals can gain a higher probability of finding prey than making an uninformed dive based on their own personal information. Thus enhanced foraging efficiency, due the ability to use the behaviour of conspecifics as indicators of prey, seems a plausible explanation as to why individuals would choose to engage in social diving behaviour in European shags.

7.2 Studying social diving behaviour

Despite the great interest in the physiological and behavioural aspects of diving to depth to catch prey, the influence of group foraging on this behaviour has received comparatively little attention. In part this is likely due to the inherent difficulty of studying these behaviours. Many species engage in social diving behaviour far out of sight of land, in locations that may vary depending on transient prey or weather fronts. Studying individuals in large groups is challenging even in terrestrial systems, and detailed study of the diving behaviour of single animals has only recently become possible due to technological developments. Attempting an observational study on a large group of individuals that are constantly diving and resurfacing is therefore even more challenging, even when these behaviours occur in relatively predictable locations. Deploying enough devices in a population whereby a suitable number of marked animals will be present within a group is also difficult. Nevertheless, studying the behaviours of individuals within these formations is vital to understanding the behavioural mechanisms of social diving.

Shag foraging rafts can often consist of over 200 birds, with individuals possessing little in the way of identifying features and arriving from multiple colonies. Deploying (and recovering) a sufficient number of tracking devices to study the behavioural rules followed by birds within the raft was therefore unfeasible. However, shags do tend to forage within sight of land and were found to display high site fidelity (**Chapter 2**). By establishing the areas in which foraging rafts were predictable (**Chapter 3**) I was able to use collective behaviour techniques to analyse the behaviour of individuals within groups of socially diving shags (**Chapter 6**). Lukeman et al (2010b) had previously used these techniques to examine the movement of two-dimensional flocks of birds on water, although their study did not examine diving behaviour or ask any particular ecological question about the

assemblages they were studying. By extending these methodologies to encompass diving behaviour, I provide the first insight into the systems governing the movement and diving behaviour of individuals within a group (**Chapter 6**).

However, while our comparison to simulation data yielded some interesting results, there are potentially some improvements to be made. While the results provide strong circumstantial evidence for the use of social information while diving, there are limits to the statistical confidence we can have about the best model due to the method used to optimise the goodness of fit measure. The method used does not penalize model complexity, as would be the case with Bayesian model selection (Xie *et al.*, 2010). This increases the uncertainty as to which set of diving and resurfacing rules best represent the data. Utilising a statistical framework to more precisely model the influence of conspecifics on movement and context dependant actions would be extremely beneficial for any future study of social diving behaviour (Delgado *et al.*, 2014).

7.3 Dive copying behaviour and producer scrounger systems

By showing that an individual's diving behaviour can be influenced by their neighbours' diving behaviour (**Chapter six**), I lend weight to the idea that information benefits may drive social diving behaviour. However, based on the simulation work carried out, these information benefits do not appear to extend to underwater interactions. Simulating underwater following behaviour did not produce the most parsimonious model. As discussed in Chapter six, this may be due to the way the simulation abstracts underwater interactions, or because following a conspecific underwater is more costly than simply copying their dive behaviour, which may be

the case if hydrodynamic benefits do not particularly improve foraging efficiency or if prey disperse after the leader has dived.

Copying behaviour is frequent in many species (Valone, 2007) and several studies have shown that animals will copy the foraging behaviour of conspecifics (Galef Jr & Giraldeau, 2001; Krebs & Inman, 1992b; Pitcher & House, 1987; Waite & Grubb, 1988). The copying of foraging decisions can be modelled as a producer-scrounger game, whereby individuals can either choose to search for food themselves (producers) or search for others who are feeding (scroungers) (Barnard & Sibly, 1981; Galef Jr & Giraldeau, 2001; Vickery *et al.*, 1991). The number of animals using each strategy will vary depending on the predictability of prey, number of conspecifics in a group, and the number of conspecifics playing each strategy. Copying behaviour is predicted to be most frequent when prey is difficult to find and takes longer to handle (Mottley & Giraldeau, 2000; Vickery *et al.*, 1991). Animals are also more likely to copy opportunistically when they can monitor their conspecifics behaviour and foraging involves some form of conspicuous behaviour (Vickery *et al.*, 1991).

Given these requirements and predictions, it seems likely that the choice about whether to dive based on personal information or whether to copy the diving behaviours of others will operate on similar principles. The act of diving is highly conspicuous and socially diving animals have ample opportunity to scan for conspecific activity as they are often required to rest on the surface after making a dive. In Chapter five I demonstrated how the ability to assess foraging success is not required for copying the dive behaviour of others to be a viable strategy. This result is similar to other group foraging studies, which also found that individuals would be attracted to any type of cue from a conspecific, not just a successful find (Barnard &

Sibly, 1981). This, along with the findings of Chapter six, showed that all the types of interactions we would expect in a producer-scrounger system can take place within foraging rafts. Animals utilise conspecific diving as indicator of local prey availability and move to dive in the immediate area around that conspecific, copying *where* they dive (Barnard & Sibly, 1981). Likewise rapidly moving prey underwater can be considered a fluctuating patch, meaning that copying *when* to dive from a conspecific will be less costly to an animal than making an uninformed sampling dive itself (Krebs & Inman, 1992a). Individuals can also directly follow a chosen conspecific on the surface, in the hopes of being led to a local prey patch. Based on these findings, groups of socially diving animals might present an interesting system with which to further apply such general models of group foraging.

7.4 Social diving and recruitment centres

In Chapters one and three I suggested that while there didn't seem to be any evidence suggesting information transfer at the colony would be useful, shag communal perches might be recruitment centres. In Chapters four, five and six I address the question of what type benefits might be gained from group foraging at the patch. I suggest that enhanced foraging efficiency due to easy availability of social information might be the main advantage of foraging rafts, and the results of Chapter six show that social information use is indeed an important component of diving in groups. However, the question remains: is the advantage gained for social information sufficient for a recruitment centre to operate?

A recruitment centre requires that successful individuals returning to a communal area benefit from recruiting conspecifics to a patch, and that less successful individuals benefit from gaining information about food discoveries by

following the individual most likely to lead them to prey. As discussed in Chapter two, this leads to two important questions: a) why should a successful individual return to the communal area? And b) why would individuals wait to be recruited rather than foraging themselves? While frequency dependence of payoffs to strategies can explain why all individuals don't just wait to be recruited (Barta & Giraldeau, 2001), it is harder to explain why shags might return to the communal perches that large groups are often seen departing from. The main activities that take place on these rocks are resting and wing-drying, with no evidence of active recruitment.

Nevertheless, large groups of shags are often seen departing from these areas, going on to form foraging rafts. It seems likely therefore that recruitment (in the sense of returning so as to be followed) is not occurring. It is possible that birds will simply follow recognisably more experienced individuals (such as older or more dominant birds) when they depart to forage. This might imply that certain individuals (possibly older or more social dominant animals) often lead groups to forage (Evans, 1982), which might also explain the seemingly spontaneous changes in foraging patch that rafts will make (flying a few hundred metres before landing to begin foraging again). However during these movements shags will "leap-frog" each other, and the individuals that initiated the move, who generally were previously at the front of the raft, end up at the back. This constant changing of positions makes the idea of certain experienced individuals leading the group unlikely.

An alternate idea is that shags choose an individual to follow at random, as this might lead them to find a better patch than they would foraging alone (Mock *et al.*, 1988; Waltz, 1982). The large-scale spontaneous departures observed may therefore be caused by a individuals randomly deciding to follow a departing individual followed by an information cascade (Simons, 2004). The "leap-frogging"

behaviour carried out by the foraging rafts may also be due to a single individual deciding to move to a different foraging patch (possibly due to lack of foraging success) and generating an information cascade, which results in the entire raft moving. However, while it has been shown that the decisions of a small number of individuals can lead to large scale group decisions (Couzin *et al.*, 2005), a move could lead the following animals to abandon a patch where they were achieving high foraging success. Copying this decision would therefore be a detrimental information cascade (Giraldeau *et al.*, 2002). If the entire group repeatedly copies the decisions of a few individuals it must be assumed there is some benefit to those following. These may be the general benefits gained from foraging in a group, as discussed in Chapters four, five and six. Alternatively, as with departures from the communal area, there might be a general assumption that the leading birds are informed in some way.

While this thesis details some of the potential advantages to diving in groups and the conditions in which it will occur, the individual decisions that actually lead to the formation and movements of foraging rafts are still poorly understood. Edge individuals were deliberately ignored in Chapter six, as it was thought that leadership effects would have complicated the results. Further study into the effect of edge individuals on the movement of individuals within the rafts, together with the large scale movements of the rafts themselves, would allow better insight into how group scale consensuses are reached in large groups of animals. Similarly, in depth study of the interactions at communal perching areas would help shed light on the behavioural mechanisms causing seemingly spontaneous group departures. This would give us better understanding of both the behaviour of foraging rafts of

European shags, and of the individual behavioural rules that can cause large foraging assemblages to form.

7.5 Information use at differing scales

The use of information to assist in the finding of prey clearly operates at several different levels. Upon leaving a colony an animal is immediately presented with broad scale choices. In the case of a European shag, a bird can choose to attempt to follow a conspecific from the colony straight to a foraging patch, head towards a communal assembly area to potentially form a foraging raft, head to join an existing assemblage (or to an area where rafts are known to form) or attempt to search for prey. If the bird decides to search for prey itself, further decisions must be made, based on the animals previous experience and current conditions. An individual will have to decide whether to forage inside or outside the main channel, which particular patch is likely to yield the best results, and how far to travel. Even upon reaching a patch there are still more decisions to be made. While foraging a shag must decide where within the patch to dive, how deep to dive, how long to remain underwater, how long to rest and how long to remain at that patch before moving. If there are conspecifics at the patch, a bird will have to decide whether to attempt to copy the dive behaviour of their conspecifics, which includes when and where to dive. They will also have to make decisions about how long to rest and when to make a more costly dive so as to take advantage of short term prey availability. As detailed in Chapter two, shags are short ranging coastal species. Other species that travel further to forage will face an even more complex series of decisions.

In this thesis, I have detailed how the availability of social information might affect some of these decisions, both at the patch and in general. This raises some interesting questions about how animals resolve differing scales of social information. Will an animal consider the decisions that will later be made at the patch when deciding on a general area to forage in? Will it choose an area based on the assumptions that it can get more detailed social information from conspecifics upon arriving? We might also ask how animals will integrate multiple conflicting sources of social information. When faced with the choice between copying a diving conspecific or following the general movements of the group, an animal will have to utilise its personal information in order to choose which cue (if any) to act on. Advancements in technology and modelling techniques will likely be vital for attempting to answer some of these questions. Detailed tracking of multiple individuals, possibly combined with animal-mounted cameras may allow better understanding into how animals utilise differing scales of personal and social information when making decisions.

7.6 Conclusions

I found that social information use at the patch may be one of the main benefits to diving in a group, as individuals can use the diving behaviour of conspecifics while making diving decisions. This shows that even small scale information use can be of great benefit for animals wishing to reduce uncertainty before making a decision. Future study of these behaviours might further investigate how the combination of these individual decisions can lead to the formation and movements of large groups of diving animals, possibly using three dimensional tracking data. This will further refine our understanding of this previously understudied behaviour.

8. Appendices



Appendix 3.1 Calculation of first passage time

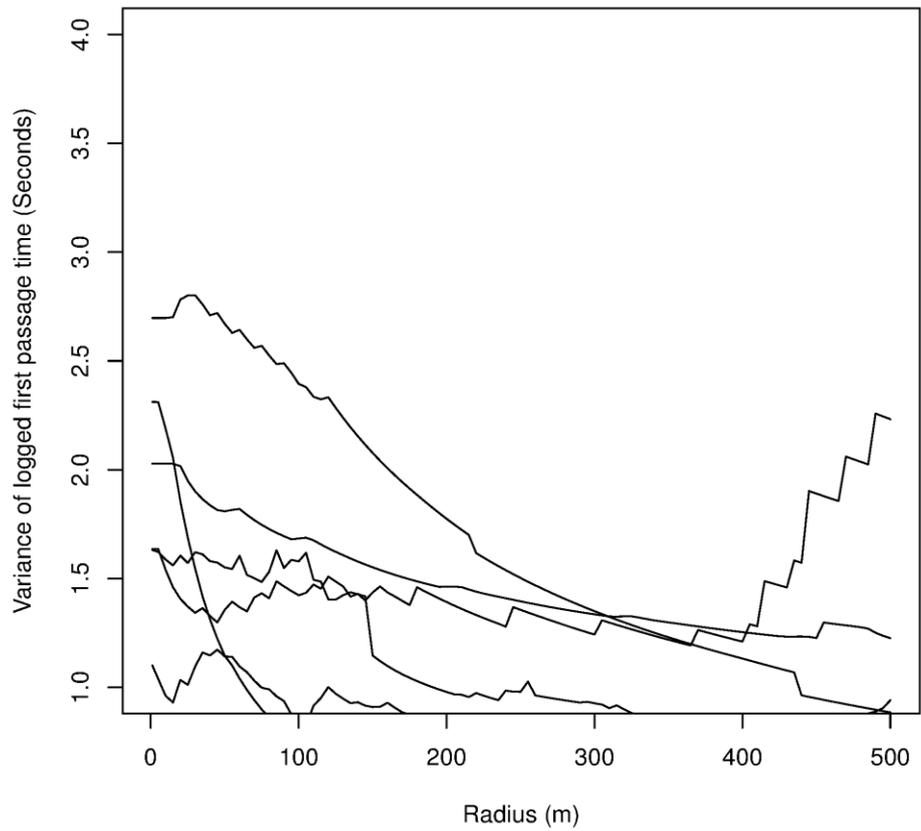


Figure A3.1: Example graph of variance in logged first-passage time. Variance is plotted as a function of radius r , of each trip of a single bird. The radii at which peaks of variance occurred were used to calculate a mean ARS scale for this individual.

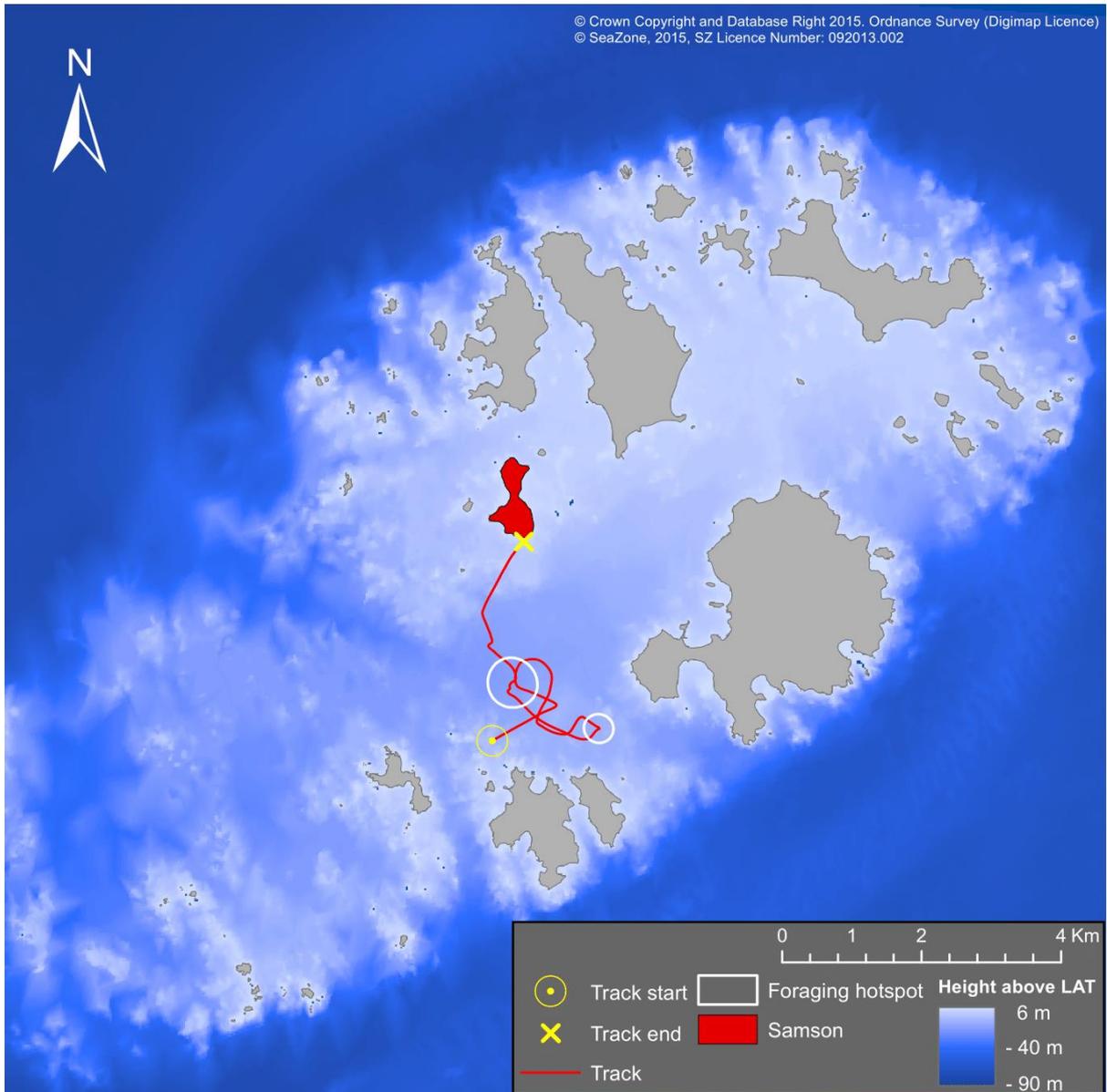


Figure A3.2: Example of a single foraging trip. Shows a bird (number 7) leaving a rock, engaging in ARS twice and returning to its' home colony. Foraging hotspots represent the top 20% of the kernel UD calculated from identified ARS for this trip, and are shown in relation to bathymetry.

Table A3.1: Mean radii at which peaks of variance of logged first passage time occur.

Bird ID	Mean Radius (m) \pm SD
1	112 \pm 338
2	136 \pm 175
3	168 \pm 413
4	60 \pm 76
5	77 \pm 169
6	23 \pm 11
7	53 \pm 133
8	39 \pm 58
9	72 \pm 171
10	183 \pm 353
11	11 \pm 353
12	17 \pm 37
13	27 \pm 52

Appendix 3.2 Models during calculation of statistics

Table A3.2: Models used during calculation of statistics. Includes full model, top model (Model 1, highlighted in bold) and models within $\Delta 2$ AICc of the top model which were model averaged to calculate final model

Model ID	Intercept	Home colony	Within raft area (1/0)	Distance from colony	Bathymetric depth	Bathymetric slope	AICc	Δ AICc	df	Weight
Full Model	1.4395	1.1964	-0.7299	-0.0001	-0.0082	0.1852	535.80	26.30	9	
1	1.5200		-0.7695				507.70	0.00	6	0.47
2	0.9409						508.40	0.64	5	0.34
3	2.0460		-0.8274				509.50	1.76	5	0.19

Appendix 5.1 Terminal fitness function

The fitness function $F(X, N, S, t, T)$ is defined as the maximum expected catch of fish between the period t and T , which an individual can maximise by making an optimal decision at each timestep, which we detail here.

At the final timestep of the model, an individual should always dive as long as this will not place them over the anaerobic threshold. Therefore let the fitness at the terminal period (where $t = T$) be:

$$F(X, N, S, T, T) = \begin{cases} \max(p_0\lambda(n, s), p_0\sigma\lambda_0 + p_0(1 - \sigma)\mu) & \text{if } x \leq x_2 - a_2 \\ 0 & \text{otherwise} \end{cases} \quad (\text{A1})$$

Where the probability of choosing an informed conspecific to copy σ is:

$$\sigma = h_0 + (h_0 - h)((h_0 - h + 1)^g) \quad (\text{A2})$$

Appendix 5.2 State transitions and dynamic programming equation

For any $t < T$ an individual must choose whether to rest, dive using personal information or copy a conspecifics diving behaviour.

If an individual chooses to rest, their fitness is:

$$v_1(X, N, S, t) = F(x', n', s', t + 1, T) \quad (\text{A3})$$

Where x' , n' and s' are how state variables change while resting:

$$x' = \begin{cases} 0 & \text{if } 0 \leq x \leq b_1 \\ x - b_1 & \text{if } b_1 \leq x \leq x_1 \\ x - b_2 & \text{if } x_1 \leq x \leq x_2 \end{cases} \quad (\text{A4})$$

$$n' = n + 1$$

$$s' = s$$

While if an individual chooses to dive, their fitness increases by the expected catch

$p_0\lambda(N, S)$ their state variables change as follows:

$$x'' = \begin{cases} x + a_1 & \text{if } 0 \leq x \leq x_1 \\ x + a_2 & \text{if } x_1 < x \leq x_2 - a_2 \end{cases}$$

$$n'' = 1 \quad (\text{A5})$$

$$s'' = \begin{cases} 1 & \text{if prey is encountered} \\ 0 & \text{if not} \end{cases}$$

Therefore if an individual chooses to dive using their own personal information, their

fitness from t to T is:

$$v_2(X, N, S, t) = p_0\lambda(n, s) + \lambda(n, s)F(x'', 1, 1, t + 1, T) + [1 - \lambda(n, s)]F(x'', 1, 0, t + 1, T) \quad (\text{A6})$$

If an animal chooses to dive using social information their fitness increases by the expected catch $\sigma p_0 \lambda_0 + (1-\sigma) p_0 \mu$ which is the probability of following an informed individual, encountering prey and successfully catching prey or following an uninformed individual, but still encountering and successfully capturing prey. Hence if an individual dives based on social information, their fitness from t to T is:

$$\begin{aligned}
v_3(X, N, S, t) = & \sigma p_0 \lambda_0 + (1 - \sigma) p_0 \mu + \sigma \lambda_0 F(x'', 1, 1, t + 1, T) \\
& + [\sigma(1 - \lambda_0)] F(x'', 1, 1, t + 1, T) \\
& + [(1 - \sigma)\mu] F(x'', 1, 1, t + 1, T) \\
& + [(1 - \sigma)(1 - \mu)] F(x'', 1, 0, t + 1, T)
\end{aligned} \tag{A7}$$

So that the optimum decision is decided by the dynamic programming equation:

$$F = (X, N, S, t, T) = \begin{cases} \max(v_1, v_2, v_3) & \text{if } 0 \leq x \leq x_2 - a_2 \\ F(x - b_2, n + 1, s, t + 1, T) & \text{if } x \leq x_2 - a_2 \end{cases} \tag{A8}$$

Appendix 6.1 Equations used in transformations

Angle of view of Sony Handycam HDR-CX190E, ϕ was calculated as follows:

$$\phi = 2\arctan\left(\frac{d_v}{2f}\right) = 2\arctan\left(\frac{3.1\text{ mm}}{5\text{ mm}}\right) = 63.3^\circ$$

where d_v is the vertical dimension of the image sensor and f is the focal length of the lens.

The camera axis angle θ was calculated for each sequence:

$$\theta = 2\arctan\left(\frac{d_s}{h}\right)$$

where d_{sh} is the horizontal distance from the observation point to the shoreline aligned with the bottom of the frame (calculated by plotting the heading of the camera from the coordinates of the observation point) and h is the height of the camera.

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