PECKING RESPONSE IN LESSER BLACK-BACKED GULL CHICKS *LARUS FUSCUS*

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Abstract

The pecking response of the Lesser Black-backed Gull (*Larus fuscus*) was investigated. This is a type of innate begging behaviour, whereby chicks peck at the red spot on the parent's bill to induce regurgitation of food. The pecking response in naïve chicks was found to be released by a diverse range of stimuli, indicating an initial flexibility in this behaviour. However, chicks' reactions were swiftly adjusted with experience, which may be adaptive in rapidly learning the distinguishing features of their parents and the natal environment, as well as a variety of food items, such that chicks can feed effectively when in competition with siblings. Pecking behaviour was robust to predetermined variation between chicks, mediated by differences in egg and parental quality.

Experiments were also conducted on the supernormal pecking response, which involves chicks pecking at a higher rate towards a long, thin, red rod with three terminal white stripes than they do towards the parental bill. Tinbergen and Perdeck (1950), who discovered this phenomenon, suggested that it was an adaptation to the angle at which a newly hatched chick crouching in the nest would first see the parental bill. This was addressed experimentally, along with the hypothesis that supernormal behaviour reflects chicks' innate feeding preferences.

Little support was found for Tinbergen and Perdeck's (1950) hypothesis. There was some evidence that supernormal pecking is an adaptation to innate feeding preferences, with chicks choosing food items that shared properties with the supernormal stimulus (the white stripes, the red colour and the thinness). However, experimental evidence could not completely refute an alternative interpretation of supernormal behaviour as a non-adaptive byproduct of the chicks' nervous system (Ramachandran, 2004).

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Chapter 1

Gulls, evolution and the study of behaviour

1.1 INTRODUCTION

The behaviour of animals has been a source of fascination to humans for millennia, as can be seen in the illustrations of animals that adorn ancient monuments the world over. In Classical Greece, Aristotle (384 - 322 B.C.) made empirical observations on animals, and many others followed his example over the centuries, from Pliny the Elder (A.D. 23 - 79), who established the concept of natural history, to Thomas Aquinas (1225 - 1274), who effectively reintroduced Aristotelian thought to Europe after the Dark Ages and thus helped to pave the way for scientific enquiry through the Renaissance to the Enlightenment (Shapin, 1996). The beginnings of the modern scientific study of animal behaviour, known as ethology (after the Greek word "èthos", meaning character), can be traced to this time, with the work of the eighteenth and nineteenth century European naturalists including Gilbert White (1720 - 1793) and Charles Leroy (1723 - 1789) (McFarland, 1999). The most important advances of this period were, however, made by Charles Darwin (1809 - 1882), whose theory of natural selection provided a framework through which the evolutionary consequences of behaviour could be understood. Darwin also published on animal behaviour, devoting an entire chapter of The Origin of Species (1859) to this subject.

The study of animal behaviour largely matured as an academic discipline in the mid-twentieth century, thanks to the work of the pioneering scientists Konrad Lorenz (1903 - 1989) and Niko Tinbergen (1907 - 1988), who together with Karl von Frisch (1886 – 1982), were jointly awarded the Nobel Prize for Physiology or Medicine in 1973. Many of the fundamental concepts of ethology are summarized in Tinbergen's (1963) influential paper in which he set out the "four whys", addressing the function, cause, development and evolutionary history of the behaviour in question. Since Tinbergen and Lorenz's time, several new fields have emerged, including behavioural ecology, which approaches Tinbergen's questions with a combination of evolutionary biology, population ecology and ethology (e.g. Krebs & Davies, 1997) and behavioural neuroscience, which looks at the neural mechanisms and cognitive processes underlying animal behaviour (e.g. Simmons & Young, 1999). Although some of ethology's "spin-offs" have proved controversial (e.g. Cosmides & Tooby, 1994; Healy & Braithwaite, 2000), it is clear today that the study of animal behaviour in its many forms is a fertile and dynamic area of research that, along with capturing the public imagination, delivers valuable insights into the world of animal species at a time when many face a precarious future as a consequence of human activities. Any understanding that can be fostered is therefore a positive step.

1.2 INSTINCT

One of the most important and controversial concepts in the study of animal behaviour is instinct. Early writers on this topic were philosophers, including René Descartes (1596 - 1650). Descartes' (1637) influential view was that animal instincts were created by God, and allowed animals to automatically adopt behaviour suitable to their environments. He also promoted the dichotomy between behaviour mediated by nature and nurture. The study of human instinct was later taken up by psychologists Sigmund Freud (1856 - 1939) and William McDougall (1871 - 1938) in the early twentieth century, although by this time Darwin had already framed his ideas on instinct in terms of animal behaviour in The Origin of Species (1859). Animal instincts later came to the attention of Tinbergen and Lorenz, with their key ideas and accounts of classic experiments described in Tinbergen's (1951) The Study of Instinct. In this work, instincts were referred to as units of innate behaviour (which was in turn described as "behaviour that has not been changed by learning processes") that are subject to natural selection (Tinbergen, 1951).

One of the problems with the study of instinct is its definition, as recognized by Darwin when he wrote that he would not attempt to define it in The Origin of Species (1859). The terms "unlearned", "innate", "predetermined" and "inherited" are sometimes used interchangeably with the word "instinct", which can lead to confusion (e.g. Beer, 1983). Moreover, certain schools of thought, notably comparative psychology, have emphasized the role of learning in the shaping of animal behaviour, thus diminishing the importance of instinctive behaviour (Lehrman, 1953), while the influential American behaviorist school of psychology rejected all reference to the cognitive processes controlling an animal's actions, and instead focused solely on the manifestation of the behaviour (Watson, 1913), effectively eliminating any consideration of instinct.

From the ethological viewpoint, Lorenz (1937, cited in Tinbergen, 1951) stated that instincts were a series of species specific, genetically determined, highly stereotyped and almost reflexive "fixed-action patterns", initiated in response to the presentation of particular features, known as "sign stimuli", or "social releasers" in the context of social behaviour. The latter may comprise only particular components of a stimulus as encountered in a natural situation. Birds including gulls and geese, for example, will retrieve and/or choose to incubate egg-like stimuli of the wrong size, colour and shape provided a threshold semblance of a natural egg stimulus is maintained (e.g. Tinbergen, 1951; 1953). In a social setting, crude and unnaturally shaped models of Three-spined Sticklebacks (*Gasterosteus aculeatus*) are sufficient to induce aggressive behaviour in breeding males of this species provided these models have a red underside (reviewed, along with other examples of social releasers, in Tinbergen, 1948). The neural processes governing the responses to such stimuli were termed "innate releasing mechanisms" (IRMs) by Lorenz (1937, cited in Tinbergen & Perdeck, 1950). These were thought to be influenced by other external sensory cues along with the relevant sign stimuli/social releasers, as well as intrinsic factors such as the animal's motivational state, so that sign stimuli/social releasers would only bring about fixed action patterns in their appropriate behavioural context.

Today these models of behaviour have been updated. The term "instinct" is often replaced by "innate", a convention adopted in this thesis, where "innate" is taken to describe behaviour that develops without obvious environmental influence (after McFarland, 1999). Fixed action patterns are now typically referred to as "motor patterns" or "motor programmes" (Margolis *et al.*, 1987; Simmons & Young, 1999), while the concept of the IRM has largely been abandoned in favour of a more flexible approach, recognising the effect of genetics and learning on innate behaviour.

1.3 THE ROLE OF GULLS IN THE STUDY OF ANIMAL BEHAVIOUR

Although gull behaviour was the subject of scientific study before Tinbergen's time (e.g. Strong, 1914; Goethe, 1937, cited in Tinbergen & Perdeck, 1950), it was principally Tinbergen's fondness for this group of birds, fostered during his childhood on the Dutch North Sea coast (Tinbergen, 1953), that put gulls at the forefront of ethological research during this field's emergence as a rigorous scientific discipline in the mid-twentieth century. Tinbergen's Nobel Prize was in no small part due to his work on the behaviour of Herring Gulls (*Larus argentatus*) (Tinbergen & Perdeck, 1950; Tinbergen, 1951; 1953) carried out while at Leiden University in the 1930s and 1940s. After his move to the University of Oxford in 1949, Tinbergen supervised and contributed to several other projects on various gull species, resulting in a number of publications (e.g. Cullen, 1957; Weidmann & Weidmann, 1958; Tinbergen, 1959; Patterson, 1965; Brown, 1967a; Dawkins & Impekoven, 1969; Verbeek, 1979). Since Tinbergen's time, the importance of gulls in the understanding of animal behaviour and related fields has not diminished, with several papers on this subject published each year, produced by research groups worldwide.

The work detailed in this thesis was largely inspired by Tinbergen's studies of gulls. Using the experiments described in Tinbergen and Perdeck's 1950 paper on Herring Gulls as a starting point, a series of tests was carried out on the pecking response in Lesser Black-backed Gull (*L. fuscus*) chicks, as reported in Chapters 3, 4 and 5. This was done with a view to establishing the mechanisms governing this behaviour, and to investigate the evolutionary pathways underlying it. In particular, the supernormal pecking response was examined (Chapter 4), and whether this behaviour relates to the feeding preferences of newly hatched young (Chapter 5). The work outlined in Chapter 2 arose as a prerequisite to these behavioural tests, as in order to gather information on factors that might influence pecking behaviour, such as chick age and laying order (see section 3.1.2), a technique was developed for hatching naïve chicks out of the nest (section 2.3.2). This in turn necessitated the thorough monitoring of part of the gull colony, so that data on these potential influencing factors, as well as predicted hatching dates, were available (section 2.3.1). Hence, a large amount of information was also collected on nesting and reproductive success in adults, all of which is considered in Chapter 2.

1.4 THE CLASSIFICATION AND EVOLUTION OF GULLS

Gulls are members of the Order Charadriiformes, commonly known as shorebirds. This is a large and diverse group of birds, comprising approximately 19 families and 350 species, depending on the definitions applied by the authors concerned (e.g. del Hoyo, 1996). Studies based on the rate of DNA evolution combined with fossil evidence, indicate that the first shorebirds arose in the Cretaceous on Gondwanaland (Cracraft, 2001; Paton *et al.*, 2003), with extant species sharing a common ancestor around 93 million years ago (Baker *et al.*, 2007). Most other modern bird lineages are also thought to have first appeared at about this time (Cracraft, 2001; Brown, 2008), with the origin of modern birds as a class (i.e. Aves) estimated at approximately 123 million years ago (Paton *et al.*, 2002).

The Charadriiformes are traditionally split into three suborders: the Lari, the Scolopaci and the Charadrii (Baker *et al.*, 2007). The gulls (Subfamily Larinae) fall into the first of these groups, making up the Family Laridae, along with the terns and noddies (Subfamily Sterninae) and the skimmers (Subfamily Rynchopinae) (International Ornithologists' Union, 2009). Other families within the Lari include the Stercorariidae (skuas and jaegers) and Alcidae (auks) (Baker *et al.*, 2007).[1] Molecular evidence indicates that three charadriiform suborders predate the Cretaceous-Tertiary boundary 65 million years ago (Paton *et al.*, 2003; Baker *et al.*, 2007), with an initial radiation of the basal lineages between approximately 80 and 65 million years ago (Paton *et al.*, 2003). However, the principal diversification of the shorebird genera is likely to have occurred after this time (Paton *et al.*, 2002; 2003; Baker *et al.*, 2007), with a period of radiation beginning around 45 million years ago which eventually gave rise to the gulls (Paton *et al.*, 2003).

Fossil evidence suggests that gulls first came into existence in the early Miocene, with the earliest remains unearthed dating from 16 to 19 million years ago (Worthy *et al.*, 2007). The molecular data are broadly consistent with these dates, although there is some uncertainty about the date at which gulls split from their sister taxon, and about which subfamily makes up this group. Most studies agree that the terns are the gulls' sister taxon (Crochet *et al.*, 2000; Ericson *et al.*, 2003; Thomas *et al.*, 2004), with some suggestion that these two groups diverged around 13.5 million years ago (Crochet *et al.*, 2000). There is also some indication, however, that the skimmers are the gulls' sister taxon (Paton *et al.*, 2003; Baker *et al.*, 2007; Fain & Houde, 2007), with a split between these groups 22.7 million years ago, following a divergence with the terns 24.4 million years ago (Paton *et al.*, 2003). The inconsistencies in the molecular evidence belie both the different genetic sequences (both nuclear and mitochondrial) and the molecular clock calibration points which are used as a basis for phylogenetic trees

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[1] The Turnicidae (buttonquails) may also be a (basal) member of the Suborder Lari, but the genetic evidence is not yet resolved (Paton *et al.*, 2003; Paton *et al.*, 2006).

constructed in each study (Crochet *et al.*, 2000; Pons *et al.*, 2005; for a review, see van Tuinen & Hedges, 2001; van Tuinen *et al.*, 2004).

The relationships between the gulls themselves are no less complicated. There is thought to be around 55 species of gull, although the exact number is subject to frequent revisions in the light of emerging molecular evidence, resulting in groups that were previously regarded as subspecies being granted full species status, and vice versa (e.g. Collinson *et al.*, 2008). The number of genera that make up the Family Laridae is also unclear. Some authors have placed all species in the genus *Larus* (e.g. Harrison, 1987), whereas others have argued for the gulls to be split. Until recently, the consensus appeared to be that most gull species were placed in the *Larus* genus, although there were a small number of genera reserved for the few species with atypical traits. These were *Rissa* (the Kittiwakes), *Creagrus* (the Swallow-tailed Gull, *C. furcatus*), *Pagophila* (the Ivory Gull, *P. eburnea*), *Rhodostethia* (Ross's Gull, *R. rosea*) and *Xema* (Sabine's Gull, *X. sabini*) (e.g. Malling Olsen & Larsson, 2004). However, now there are calls for genera that were formally applied but have since fallen out of use to be resurrected on the basis of molecular phylogenetics (Crochet *et al.*, 2000; Pons *et al.*, 2005). Such advice is being partially followed, with the recent reinstatement of the genus *Chroicocephalus* for the masked species (e.g. the Black-headed Gull), and *Hydrocoleus* for the Little Gull (*H. minutus*)[2] (American Ornithologists' Union, 2009; British Ornithologists' Union, 2009; International Ornithologists' Union, 2009).[3]

Such taxonomic confusion can partly be attributed to the fact that classification was traditionally based on comparative studies of morphological and/or behavioural traits (for relatively recent examples of

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[2] The exact classification used varies between countries. The British Ornithologists' Union, for example, has not currently adopted the recommended reclassification (Pons *et al.*, 2005) of the hooded species (Fig. 1.1) from *Larus* to *Leucophaeus*, although the American Ornithologists' Union has.

[3] For a full list of gull species names used in this text, and of previously used and alternative names, see Appendix I.

these techniques, see Cane, 1994; Chu, 1998). As a group, gulls exhibit relatively few differences between species, but substantial intraspecific variation, such that it is often difficult to characterise species specific traits (Collinson *et al.*, 2008). Similarly species that are geographically isolated may appear practically identical, for example the Herring Gull and the American Herring Gull (*L. smithsonianus*), whereas those that breed sympatrically can be much easier to tell apart (Malling Olsen & Larsson, 2004). Moreover, species identification is confounded by the prevalence of hybridization (Tinbergen, 1953; Ingólfsson, 1987; Good *et al.*, 2000; Good, 2002; Liebers *et al.*, 2004; Malling Olsen & Larsson, 2004; Gay *et al.*, 2007; 2009; Collinson *et al.*, 2008; Vigfúsdottir *et al.*, 2008), as, in common with other birds, species barriers are often initiated and maintained through interspecific behavioural differences, mediated by cultural transmission and the influence of sexual imprinting in mate choice (Tinbergen, 1953; Brown, 1967a; Harris, 1970; Grant & Grant, 1997; Liebers *et al.*, 2001; Gay *et al.*, 2007). Therefore, interbreeding and the production of viable young are possible, and in some zones, hybrid individuals outnumber members of the parent species (Good *et al.*, 2000). However, due to preferences for particular physical or behavioural characteristics, hybrid offspring can be at a selective disadvantage when it comes to attracting mates (Crochet *et al.*, 2003).

Although studies based on molecular data may also be partially obscured by hybridization (Crochet *et al.*, 2002; 2003; Liebers *et al.*, 2004; Given *et al.*, 2005; Collinson *et al.*, 2008), they are proving a useful tool in helping to unpick species differences and hence elucidate the phylogenetic relationships of the gulls (Fig. 1.1). These data confirm the subtleties in distinguishing between species, such that reproductive isolation does not necessarily imply genetic divergence (Liebers *et al.*, 2004), and strong interspecific genetic similarities may exist even when species are reproductively isolated (Crochet *et al.*, 2002; Given *et al.*, 2005).

Based on morphological distinctions, gulls have often been placed in two groups: the large, white-headed gulls resembling the Herring Gull, and the smaller masked gulls, such as the Laughing Gull (*Leucophaeus atricilla*) (e.g. Cramp & Simmons, 1983; del Hoyo *et al.*, 1996). Molecular data indicate, however, that the hood is an ancestral trait among gulls (Crochet *et al.*, 2000; Pons *et al.*, 2005), and that this has been subsequently lost by various species throughout the Family Laridae (Given *et al.*, 2005). However, the dark-headed gulls can be split into three distinct clades (the black-headed species, the hooded species and the masked species) (Fig. 1.1) (Crochet *et al.*, 2000; Pons *et al.*, 2005).[4] There is also evidence of convergent evolution, resulting in gulls with dark body plumage (e.g. the Lava gull, *L. fuliginosus*), belonging to different clades, while the white-headed Audouin's Gull (*Ichthyaetus audouinii*) falls in the black-headed species group, rather than with the large white-headed gulls (Fig. 1.1), as had previously been assumed (Crochet *et al.*, 2000; Pons *et al.*, 2005). Likewise, species with very different plumage characteristics have been shown to be closely related (e.g. the Ivory Gull and Sabine's Gull), with their physical dissimilarities arising as a result of divergent selection pressures (Fig. 1.1) (Crochet *et al.*, 2000).

Although the Laridae diverged from their sister families in the Miocene, most speciation amongst the gulls appears to have taken place much more recently, in the Pliocene and Pleistocene. Genetic studies indicate that the Kittiwakes diverged from the other gulls approximately 3.3 million years ago (Paton *et al.*, 2003), before splitting from each other approximately two million years ago (Crochet *et al.*, 2000). The Ivory Gull and Sabine's Gull form a discrete clade, and are thought to have branched from each other about two million years ago as well (Crochet *et al.*, 2000). Most other species diversified in the last million years (Crochet *et al.*, 2000), with the radiation of the large white-headed gulls estimated to have occurred between 400,000 and 100,000 years ago (Liebers *et al.*, 2001; Crochet *et al.*, 2003), and the masked gulls thought to have shared a common ancestor less than 600,000 years ago (Given *et al.*, 2005).

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[4] There is sometimes resistance to the findings based on molecular techniques (e.g. the work of Given *et al.*, 2005, disputed by Bourne, 2006, and defended by Baker & Given, 2006).

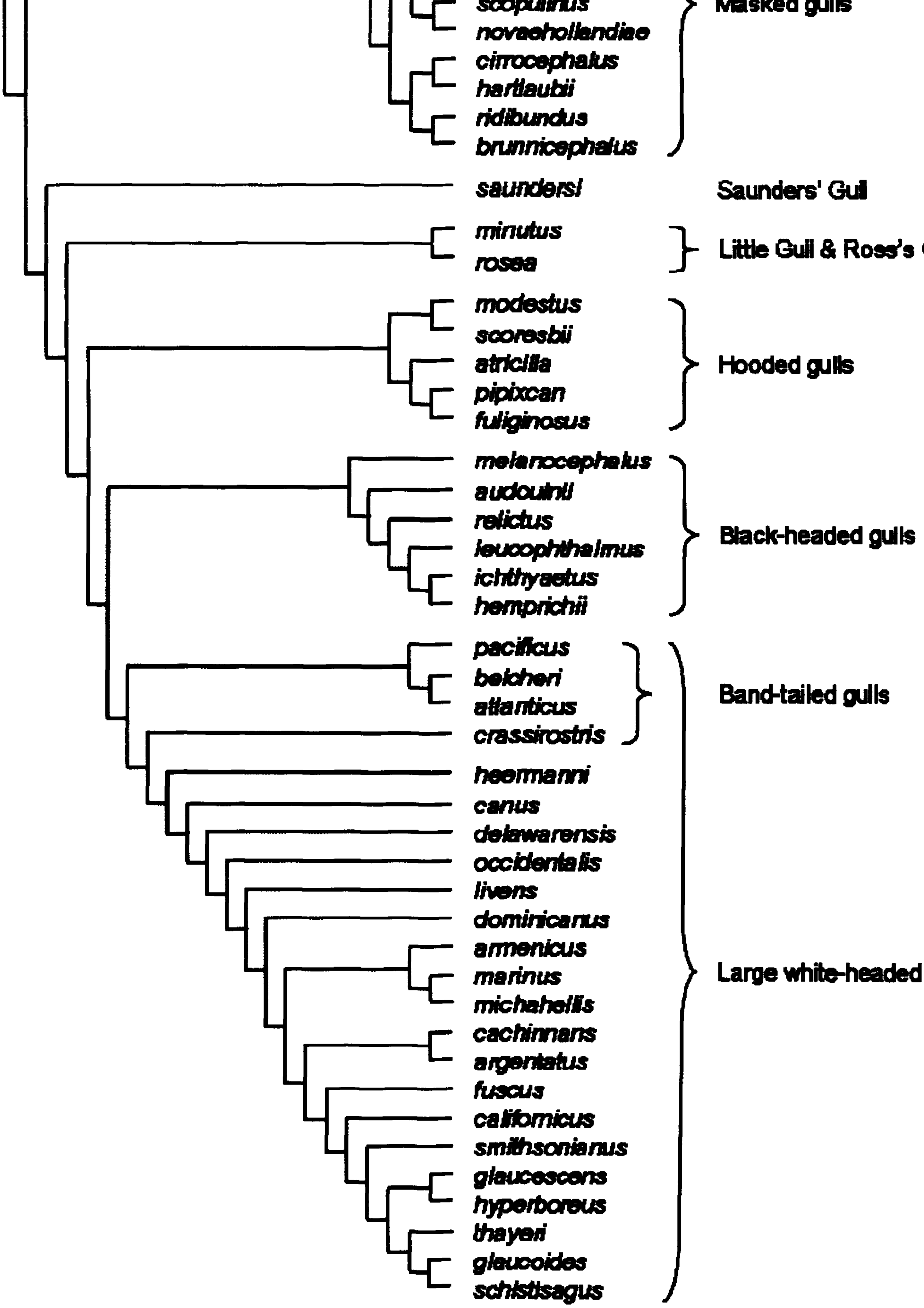

Fig. 1.1. A phylogenetic tree of the relationships between the gulls based on mitochondr

DNA. Branch lengths are not proportional to time. Adapted from Pons *et al.* (2005).

The pattern of speciation amongst the large white-headed gulls has received particular attention in recent years (e.g. de Knijff *et al.*, 2001; Liebers *et al.*, 2001; 2004; Crochet *et al.*, 2002; 2003; Liebers & Helbig, 2002; Pons *et al.*, 2004; Gay *et al.*, 2005; 2007; 2009). This is partly because of evidence that the well known "ring-species hypothesis" (Mayr, 1963) is not correct (de Knijff *et al.*, 2001; Liebers *et al.*, 2001; 2004; Crochet *et al.*, 2002). This theory holds that the large white-headed gulls originated in the Aralo-Caspian region, and then spread northwards, where they gradually spread to the east and west around the North Pole, progressively differentiating into species as the distances between populations became greater, although interbreeding and thus gene flow between neighbouring groups of birds took place. The ends of the circumpolar ring were thus thought to be the Lesser Black-backed Gull in north-west Europe, and the Herring Gull, which was thought to have crossed the Atlantic from North America to colonise the same parts of Europe as the Lesser Black-backed Gull after the Last Glacial Maximum. The Herring Gull and Lesser Black-backed Gull were thus thought to be in full reproductive isolation from each other as end points of the ring.

This model has been called into question on the basis of molecular evidence, which indicates that large white-headed gulls evolved from two ancient refugia, one in the Aralo-Caspian region, and one in the North Atlantic (Liebers *et al.*, 2004). A circumpolar ring is thought to have formed, but the end points do not meet. Furthermore, the Herring and Lesser Black-backed Gulls do not make up these end points, and neither invaded from North America. They are instead closely related species between which gene flow occurs. A ring may yet be formed, however, as Lesser Black-backed Gulls colonize North America and come into contact with the American Herring Gull, although it is not known if these species are reproductively isolated from each other (Liebers *et al.*, 2004).

1.5 THE LESSER BLACK-BACKED GULL

The study species in this thesis, the Lesser Black-backed Gull, was chosen for two main reasons. Firstly, there is a large breeding colony with easily accessible nests on Flat Holm Island, within easy reach of Cardiff University (section 2.2.1). The second reason was this species' close phylogenetic relationship with the Herring Gull. Tinbergen and Perdeck's (1950) classic paper on the pecking response in Herring Gull chicks was the starting point for much of the work detailed in Chapters 3, 4 and 5. The similarities between the Herring Gull and Lesser Black-backed Gull have frequently been noted (e.g. Tinbergen, 1953; Brown, 1967a). Furthermore, in common with all the large white-headed gulls in the monophyletic clade from the Western Gull (*L. occidentalis*) to the Slaty-backed Gull (*L. schistisagus*) (Fig. 1.1), both Herring and Lesser Black-backed Gulls have a red spot at the gonys on the lower mandible of the bill. Tinbergen examined how this feature affects chick begging (Tinbergen & Perdeck, 1950), while subsequent studies have investigated its influence on other aspects of behaviour, in species other than the Herring Gull (e.g. Morales *et al.*, 2009 who worked on the Yellow-legged Gull, *L. michahellis*). These studies considered Tinbergen's findings relevant to their own, and it was thus thought appropriate to do the same in this thesis.

Like all the large white-headed gulls except the Kelp Gull (*L. dominicanus*), the Lesser Black-backed Gull inhabits only the northern hemisphere. As its name suggests, adults of this species have a dark, slaty-grey to black coloured mantle. Other distinguishing features include yellow legs and a red orbital ring. Lesser Black-backed Gulls exhibit clinal variation in the darkness of their mantle, and other morphological traits, such as wingspan (Malling Olsen & Larsson, 2004). Populations also differ in their migratory strategies. This variation has provoked a debate about how to classify the Lesser Black-backed Gull, with particular focus on how many subspecies are found (Liebers & Helbig, 2002; Collinson *et al.*, 2008). There has been some suggestion that there are five subspecies of Lesser Black-backed Gull;

graellsii, intermedius, fuscus, heuglini and *taimyrensis,* while others have proposed that each of these groups be granted full species status (Liebers & Helbig, 2002; Collinson *et al.*, 2008). Presently, based on recent genetic evidence, only *graellsii, intermedius* and *fuscus* are considered subspecies of *L. fuscus,* with *heuglini* and *taimyrensis* classified as subspecies of *L. heuglini* (Malling Olsen & Larsson, 2004; Collinson *et al.*, 2008).

L. f. fuscus is the smallest and darkest of the Lesser Black-backed Gulls. It achieves full adult plumage three years after hatching, and has a slenderer bill, relatively longer wings and shorter legs compared to the other *L. fuscus* subspecies (Malling Olsen & Larsson, 2004). As its alternative name, the Baltic Gull, suggests, this subspecies largely breeds on the Baltic coasts of Finland and Sweden, with a small population on the north-west Russian coast, before migrating to East Africa for winter. Of all the *L. fuscus* subspecies, *L. f. fuscus* has the smallest population (possibly less than 10,000 breeding pairs) and has experienced a strong decrease in numbers in recent years to the extent that it is now considered threatened (Hario, 1994; 2006; Hario *et al.*, 2004; Malling Olsen & Larsson, 2004). This reduction might in part be linked to pesticide use at its wintering grounds. There is evidence that the chemicals involved are passed on to embryos in the egg and cause liver failure in young chicks (Hario *et al.*, 2004).

L. f. intermedius and *L. f. graellsii* are morphologically and behaviourally more similar to one another than they are to *L. f. fuscus* to the extent that some argue they should be classified as a single subspecies (Sangster *et al.*, 1999, cited in Collinson *et al.*, 2008). Generally speaking, *intermedius* has a darker mantle than *graellsii,* but there is considerable overlap between subspecies (Malling Olsen & Larsson, 2004). Both take four years to attain adult plumage. *Intermedius* and *graellsii* both breed in north-west Europe, and largely winter in south-west Europe and north-west Africa, although some Icelandic birds migrate to the eastern USA (Malling Olsen & Larsson, 2004). Populations of both subspecies have experienced substantial growth since the mid-twentieth century, bringing today's numbers (*intermedius* and *graellsii* combined) to around 300,000 pairs globally (Malling Olsen & Larsson, 2004). *L. f. graellsii* is the subspecies of Lesser Black-backed Gull found in Britain, which hosts approximately 110,000 pairs during the breeding season (Mitchell *et al.*, 2004). As the work detailed in the following chapters was carried out with the Lesser Black-backed Gull in Wales, *L. f. graellsii* is thus the subspecies described therein.

Chapter 2

Nesting behaviour, phenotypic quality and reproductive success in Lesser Black-backed Gulls (*Larus fuscus*)

2.1 INTRODUCTION

The expression of gull chick pecking and feeding behaviour, examined in detail in Chapters 3, 4 and 5, is potentially affected by several factors. Some of these are intrinsic to the chick (section 3.1.2.2), such as ontogenetic changes to behaviour (Groothuis, 1989b), while others are extrinsic (section 3.1.2.1), for example egg laying order and size (Alquati *et al.*, 2007). The work detailed in this chapter describes methods developed to assess the role of as many of these factors as possible in the behavioural responses examined in Chapters 3, 4 and 5, through the careful monitoring of nesting behaviour in a population of Lesser Black-backed Gulls (*Larus fuscus*), and the controlled rearing of a number of their chicks. The data collected also revealed several trends in the nesting behaviour of this species, and helped identify reliable predictors of reproductive success.

2.1.1 Breeding biology of gulls

Like more than 95% of seabirds (Danchin & Wagner, 1997), the majority of gull species nest colonially (Malling Olsen & Larsson, 2004).[5] Most species inhabit temperate regions, where pairs assemble to breed once per year (Tinbergen, 1953; Malling Olsen & Larsson, 2004), although species found solely in the tropics, such as the Swallow-tailed Gull (*Creagrus furcatus*) and the Lava Gull (*Leucophaeus fuliginosus*), reproduce all year round (Snow &

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[5] Some species of gulls, for instance the Lava Gull, do not nest colonially (Snow & Snow, 1969), while others, such as the Yellow-footed Gull (*L. livens*), American Herring Gull (*L. smithsonianus*) and Common Gull (*L. canus*) nest both colonially and in isolation (Burger & Lesser, 1980; Götmark & Andersson, 1984; Vermeer & Devito, 1987; Spear & Anderson, 1989).

Snow, 1967; 1969; Harris, 1970). In seasonally breeding species, individuals arrive at their colonies during the spring, about a month before copulation starts, during which time they assess nest sites, court their mates, and demarcate their territories (Tinbergen, 1953; 1959; Moynihan, 1958; Beer, 1963; Patterson, 1965; Bongiorno, 1970; Burger & Shisler, 1978; Montevecchi, 1978; Panov, 2009). While movement of nest location between nesting attempts (both within and between colonies) is sometimes seen, especially amongst young or unsuccessful pairs (Chabryzk & Coulson, 1976, Danchin *et al.*, 1998; Naves *et al.*, 2006; Parejo *et al.*, 2006), gulls usually exhibit a high degree of nest site fidelity, returning year after year to the same position in their colony (Tinbergen, 1953; Bongiorno, 1970; Chabryzk & Coulson, 1976; Verbeek, 1979; but see Burger, 1974). Gulls (especially males) can also be strongly philopatric, frequently recruiting to a site (establishing a breeding territory for the first time) within 200 m of that where they hatched (Chabrzyk & Coulson, 1976; Spear *et al.*, 1998; but see Coulson & Coulson, 2008a). Colonies are also subject to immigration and emigration from young birds, with a number of first time breeders deciding not to return to their natal colony and instead recruiting to colonies elsewhere (Parsons & Duncan, 1978; Bosch *et al.*, 2000; Oro & Ruxton, 2001; Coulson & Coulson, 2008a; Gaston *et al.*, 2009). Choice of colony may be constrained by food availability, which is thought to influence, and ultimately limit, colony size (Furness & Birkhead, 1984; Oro *et al.*, 2004).

Breeding is deferred in gulls (and many other seabirds), such that reproduction does not occur until individuals have reached a minimum of two to three years of age in smaller species, and three to four years in larger species (Spaans, 1971; Mills, 1973; Chabrzyk & Coulson, 1976; Coulson *et al.*, 1982; Pyle *et al.*, 1997; Mills *et al.*, 2008), although the average age of first breeding is usually one to two years greater than this (Chabrzyk & Coulson, 1976; Pyle *et al.*, 1997; Gaston *et al.*, 2009). Several factors are thought to contribute to this delay, including the time needed to acquire sufficient foraging skills for raising a brood (Spaans, 1971; Chabrzyk & Coulson, 1976; Coulson *et al.*, 1982; MacLean, 1986), competition faced during recruitment

(Coulson *et al.*, 1982), and the elevated risk of mortality incurred as a cost of reproduction (Reid, 1988; Golet *et al.*, 1998). The latter is particularly pronounced for individuals breeding at a young age, and thus has the potential to significantly curtail lifetime reproductive success relative to that of individuals that defer reproduction for a longer period (Pugesek, 1983; 1987; Pyle *et al.*, 1997; Cam *et al.*, 2000).

Prebreeders typically spend time at colonies prospecting for suitable nest sites in the years before recruitment (Cadiou *et al.*, 1994; Danchin *et al.*, 1998; Spear *et al.*, 1998, Boulinier *et al.*, 2008). They are apparently attracted to particular breeding patches by the presence of reproducing conspecifics (Brown, 1967b; Chabrzyk & Coulson, 1976; Oro & Pradel, 2000; Greene & Stamps, 2001; Martínez-Abraín *et al.*, 2001; Oro, 2008), and can use information gathered on the reproductive success of these pairs as a cue on which to the base their decision about where to breed (Boulinier & Danchin, 1997; Danchin *et al.*, 1998; Suryan & Irons, 2001; Boulinier *et al.*, 2008). Recruitment may occur more than a year before breeding takes place, with pairs defending territories but not producing any eggs (Chabryzk & Coulson, 1976). Even after reproduction commences, pairs sometimes reproduce intermittently, in a behavioural strategy that may be related to their phenotypic quality (Kadlec & Drury 1968; Pugesek & Wood, 1992; Pons & Migot, 1995; Calladine & Harris, 1997; Annett & Pierotti, 1999; Oro & Pradel, 2000).

Gulls are again typical seabirds in that they form socially monogamous pairs, and often breed with the same partner through their entire reproductive life, barring death of their mate (Tinbergen, 1953; 1959; Coulson, 1966; Pierotti, 1981). Divorce does occur, particularly in young or previously unsuccessful breeders, but it entails the cost of a reduction in reproductive success in the years immediately following re-pairing, such that remaining in an established partnership is usually advantageous (Coulson, 1966; Mills, 1973; 1994; Naves *et al.*, 2006). Pairs thus normally comprise individuals of approximately the same age that have recruited together (Coulson, 1966; Mills, 1973; Chabrzyk

& Coulson, 1976; Coulson *et al.*, 1982; Vieyra *et al.*, 2009). Mate choice is thought to operate through various mechanisms, including sexual selection that leads to assortative mating based on size and the colour of the integument (Helfenstein *et al.*, 2004a; Gay *et al.*, 2007; 2009; but see Good *et al.*, 2000). Year on year decisions about whether to remain with the same partner depend on other factors, such as breeding success in previous seasons (Coulson, 1966; Naves *et al.*, 2006), nest site fidelity (Naves *et al.*, 2006), and the frequency of courtship feeding (Fig. 2.1), which is thought to provide an honest indicator of quality in males (Tasker & Mills, 1981; Furness & Monaghan, 1987; Mills, 1994; Helfenstein *et al.*, 2003b). Extra-pair copulations, some of which appear forced, are not infrequent in gulls (Pierotti, 1981; Mills, 1994; Bukacińska *et al.*, 1998; Gilbert *et al.*, 1998), but the level of extra-pair paternity is very low (Bukacińska *et al.*, 1998; Gilbert *et al.*, 1998; Helfenstein *et al.*, 2004b). This could be because females are able to control the level of cloacal contact that occurs through certain body movements and by similarly unbalancing males (Helfenstein *et al.*, 2003a; Velando, 2004), while they are also known to eject sperm from the cloaca following copulations (Helfenstein *et al.*, 2003a; Wagner *et al.*, 2004).

Fig. 2.1. A male Lesser Black-backed Gull provides his partner with courtship food, Flat Holm, May 2008.

2.1.2 Nest site selection

With the exception of the Kittiwakes (*Rissa* spp.) and Swallow-tailed Gulls, which are adapted to nest on sheer cliff faces (Cullen, 1957; Hailman, 1965), most gulls are ground nesting birds that require at least a substantial ledge if any form of nesting close to a descent is to occur, as their chicks have not evolved to avoid the dangers of falling from the nest (Cullen, 1957). The nests of ground nesting species are reasonably simple, ranging from a scrape with little gathered nesting material, to a small bed of vegetation arranged in a shallow cup shape (Fig. 2.8) (Tinbergen, 1953; Beer, 1963). Gulls exhibit a considerable degree of plasticity in their nest site selection, which is reflected in both the wide and labile geographic ranges of many species,[6] and the variety of nesting habitats colonized on a more local level (Burger & Gochfeld, 1981a; 1985; 1987; 1988; Vermeer & Devito, 1987; García Borboroglu &

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[6] Geographic range is also determined by other factors, such as food availability. Species with a high degree of dietary specialization, for example Olrog's gull (*L. atlanticus*), may be constrained therefore in their habitat choices (García Borboroglu & Yorio, 1997).

Yorio, 2004a; 2004b; Skórka *et al.*, 2006). This, along with their abilities to adapt their feeding behaviour (section 5.1.1), has contributed to gulls' exploitation of nest sites in man-made environments, including industrial, commercial and domestic buildings (Monaghan & Coulson, 1977; Raven & Coulson, 1997; Skórka *et al.*, 2006). The range of habitats utilized by gulls frequently leads to sympatric nesting with other birds, including other gull species (Brown, 1967a; 1967b; Burger, 1974; Burger & Shisler, 1978; Yorio *et al.*, 2001; Ellis & Good, 2006; Panov, 2009), although nearest neighbours are usually conspecifics (Burger, 1974; Burger & Gochfeld, 1985). Such close proximity of different gull species can in turn lead to hybridization (Tinbergen, 53; Ingólfsson, 1987; Good *et al.*, 2000; Good, 2002; Malling Olsen & Larsson, 2004; Collinson *et al.*, 2008; Vigfúsdottir *et al.*, 2008).

Despite the observed plasticity in choice of breeding habitat, gulls do exhibit preferences for nest sites with particular properties. Typically, some degree of nest cover, usually in the form of vegetation, is desirable, and complements the function of the nest in helping parents to shield eggs and chicks against predators and climatic fluctuations (Burger & Shisler, 1978; Hansell & Deeming, 2002; García Borboroglu & Yorio, 2004a; Kim & Monaghan, 2005; Kazama, 2007). Pairs avoid dense vegetation, however, in order to allow space for detecting and attacking predators, and an easy passage for chicks to flee unhindered by entanglement in thick undergrowth (Burger, 1974; Davis & Dunn, 1976; Burger & Shisler, 1978; Burger & Gochfeld, 1981a; 1985; Bosch & Sol, 1998; García Borboroglu & Yorio, 2004b; Skórka *et al.*, 2006). Indeed, such intermediate nest cover has been found to be associated with high levels of chick survival (Davis & Dunn, 1976). Other factors, such as the risk of tidal flooding and the proximity to feeding grounds, may also influence nest site selection (Burger & Shisler, 1978; Lee *et al.*, 2008).

Such preferences underline how gulls can maximize the probability of successful breeding through the selection of a nest site in a safe, stable environment. Colonial breeding is sometimes also thought to contribute to such an environment, by imparting protection against predators through the dilution of the probability that they target any one individual (Hamilton, 1971), and the simultaneous mobbing of predators by several breeders (Götmark & Andersson, 1984; Anderson & Hodum, 1993; Hernández-Matías *et al.*, 2003). Further advantages attributed to colonial breeding are the availability of social information about resources (Ward & Zahavi, 1973; King & Cowlishaw, 2007; Seppanen *et al.*, 2007), and access to extra-pair mates (Danchin & Wagner, 1997). Such benefits might have selected for the evolution of coloniality (Danchin & Wagner, 1997; but see Wagner *et al.*, 2000). However, there are also several potential disadvantages to colonial breeding, the extent of which (as with the advantages) might depend on external environmental factors such as food availability, or intrinsic properties of the colony, such as its size and density. These drawbacks include an increase in intraspecific competition, predation or infanticide, disease transmission, cuckoldry, and the possibility that large, conspicuous groups actually enhance the risk of egg and chick loss by attracting predators (Rodgers, 1987; Danchin & Wagner, 1997; Varela *et al.*, 2007; Ashbrook *et al.*, 2008).

In gulls, it appears that coloniality does benefit individuals through the provision of socially transmitted cues about breeding success (as discussed), and the presence of intruders, by neighbours monitoring each others' vigilance behaviour (Beauchamp, 2009). The impact of predation also appears to be diluted in dense colonies compared to birds nesting in loose aggregations or in isolation (Götmark & Andersson, 1984; Oro, 1996a; but see Burger, 1974). However, there is little evidence that information on feeding sites is shared (Evans, 1982a), and while extra-pair copulations occur, they are largely ineffective in producing young (section 2.1.1). However, there are numerous reports that many of the disadvantages of colonial breeding, namely intraspecific predation of eggs and chicks, competition, nest-parasitism, aggression, and the spread of pathogens, have far-reaching effects on individual reproductive success (Brown, 1967b; Burger, 1974; Hunt & Hunt, 1975; Parsons, 1975a; Davis & Dunn, 1976; Schoen & Morris, 1984; Spaans *et al.*, 1987; Brouwer *et al.*, 1995; Duda *et al.*, 2003; 2008).

A means by which the costs of coloniality can be offset is the synchronization of breeding, whereby colony members engage in copulation, egg laying and chick rearing at the same time as their neighbours (Davis & Dunn, 1976; Parsons, 1976; Panov, 2009). This behaviour has the dual effect of both further diluting the role of interspecific predation in the loss of eggs and chicks, and reducing the danger of breeding failure due to intraspecific interference (Hunt & Hunt, 1976a; Kazama, 2007). Infanticide and cannibalism of eggs and chicks is a major cause of offspring mortality in several gull species (Paynter, 1949; Brown, 1967b; Davis, 1975a; Hunt & Hunt, 1975; 1976; Davis & Dunn, 1976; Montevecchi, 1977; Schoen & Morris, 1984; Brouwer *et al.*, 1995; but see Burger, 1974), and is thus a major drawback of colonial breeding, especially in over-crowded colonies (Davis & Dunn, 1976).[7] Chicks are not always eaten, but are often simply attacked and killed for wandering into neighbouring territories (Emlen, 1956; Fordham & Cormack, 1970; Hunt & McLoon, 1975; Hunt & Hunt, 1976a; Montevecchi, 1977; Fetterolf, 1983a). Chicks are more conspicuous and hence more likely to be picked off by the predatory behaviour of members of the same or different species if they are the only young present in a colony, that is, if they hatch before or after the majority of other chicks (Hunt & Hunt, 1976a; Brouwer *et al.*, 1995). Synchronization thus lowers the risk of such losses (Burger, 1980; Fetterolf, 1983a; 1984). When conspecific parents are engaged in caring for their own brood they are less likely to seek opportunities to predate neighbours. Furthermore, even if young chicks do wander, they are more likely to be adopted rather than attacked by other parents if they too have chicks of the same age, as parental recognition is not well developed early in a chick's life (Tinbergen, 1953; Holley, 1981; Knudsen & Evans, 1986; Pierotti & Murphy, 1987; Brown, 1998; Bukaciński *et al.*,

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[7] Some authors attribute the high levels of infanticide recorded to an artefact of investigator disturbance, whereby human presence frightens chicks into neighbouring territories, or leaves young chicks undefended if their parents fly away from the nest (Gillet *et al.*, 1975; Fetterolf, 1983a; 1983b; but see Brown & Morris, 1995). It has been suggested that in the absence of investigator disturbance, breeding gulls cooperate with other pairs and do not prey on each others' chicks (Shugart & Fitch, 1987).

2000). Thus, by the time all synchronously hatched chicks are old enough to be perceived as foreign by neighbouring adults, they are better able to escape from, and defend themselves against, attacks.

Synchronized breeding may also have other benefits, including access to a pool of information about food sources from other breeding individuals, which may not be available to pairs reproducing earlier or later in the season (Emlen & Demong, 1975). Synchronization is likely to be in part brought about by social facilitation, such that observing nest building, courting and copulations by other pairs (Fig. 2.2) stimulates breeding in neighbouring individuals (Brown, 1967b; Chabaryzk & Coulson, 1976; Burger, 1979; Panov, 2009). The timing of breeding may also be influenced by other extraneous factors, however, such as the weather, tides and food availability (Burger & Shisler, 1978; Burger, 1979).

Fig. 2.2. A breeding pair of Lesser Black-backed Gulls copulates next to their nest (right) on Flat Holm, May 2008, while an incubating bird looks on.

2.1.3 Nest distribution

The creation and maintenance of a breeding territory is energetically taxing. Competition encountered by first time breeders at a colony can be intense (Chabryzk & Coulson, 1976), whilst costly aggressive interactions, including fighting, calling and displacement activities such as grass pulling, are regularly seen in even the most established pairs (Fig. 2.3) (Tinbergen, 1953; 1959; Emlen, 1956; Burger & Beer, 1975; Southern, 1981; Butler & Janes-Bulter, 1982; Bukacińska & Bukaciński, 1994; Pierotti & Annett, 1994). These behaviours appear to be necessary throughout the season (during which the significant demands of rearing a brood must also be addressed) to prevent territorial encroachments, involving the theft of nesting materials, predation of eggs or chicks, and extra-pair copulations with an individual's mate (Burger & Beer, 1974; Bukacińska & Bukaciński, 1994; Panov, 2009). Phenotypically inferior pairs, therefore, struggle to secure and successfully breed at a nest site in a patch favoured by superior birds. Subordinates may thus be relegated to different, non-preferred, and often suboptimal areas, in a process that has implications for the distribution of nests in the colony.

Fig. 2.3. Breeding Lesser Black-backed Gulls fighting over territory, while other birds look on or incubate their eggs. Flat Holm, May 2008.

Several studies have shown that the spatial distribution of nests within seabird colonies, and that of communally nesting birds in general, is clumped (Patterson, 1965; Verbeek, 1979; Burger & Gochfeld, 1980; Anderson & Hodum, 1993; Barbour *et al.*, 2000; Jovani & Tella, 2007). Some of this aggregation is habitat-mediated and hence necessitated by the features of the nesting environment (Danchin & Wagner, 1997), but there is also evidence that breeding pairs distribute themselves according to their quality, indicating that certain nest sites might shift the balance in the trade-off between the costs and benefits of colonial breeding in gulls, assuming that individuals occupy nest sites that maximize their fitness (Fretwell & Lucas, 1970). A common observation is that older, well-established, successful and higher quality birds nest centrally in a colony, where they are better protected against predators (but see Montevecchi, 1977; Brunton, 1997), while younger and less successful pairs are confined to the edges, in the so-called "central-periphery" distribution (Coulson, 1968; Dexheimer & Southern, 1974; Parsons, 1976; Montevecchi, 1978; Pugesek & Diem, 1983; Kazama, 2007).

Other models of nest spacing to which certain gull colonies have been found to conform include the "ideal free" and "ideal despotic" distributions (Fretwell & Lucas, 1970). The ideal free model hypothesizes that decisions about nest placement are made according to the benefits conferred by particular nest sites. When these are attenuated by high density nesting, it becomes profitable for pairs to choose sites in formerly less optimal areas with a lower nest density. American Herring Gulls (*L. smithsonianus*) nesting in eastern Canada and Black-legged Kittiwakes (*R. tridactyla*) in Alaska have been found to nest in a manner consistent with the ideal free distribution (Pierotti, 1982; Suryan & Irons, 2001). The ideal despotic model, on the other hand, suggests that nest choice is dictated by the competitive exclusion of subordinate individuals from the territories of dominants. Assuming that dominant birds occupy the best habitats, the weaker, poorer quality individuals are therefore forced to breed in sub-optimal areas, with detrimental consequences for their fitness. Studies of Yellow-legged Gulls (*L. michahellis*) on the Mediterranean coast of France and Spain indicate that nests are spaced according to this distribution, with recruits obliged to nest in areas adjacent to their preferred breeding patches following struggles with established, dominant pairs (Bosch & Sol, 1998; Vidal *et al.*, 2001; Oro, 2008). Ideal despotic nesting has also been found in other species of seabird (Kokko *et al.*, 2004). A further model that has been identified as applying to other seabirds, and which therefore might also apply to gulls, is the "central-satellite" distribution, where low quality birds attempt to nest close to their high quality counterparts, who do not necessarily nest centrally, in order to obtain a share of the commodities, such as access to better nest sites or mates for future years, available to individuals breeding in these areas (Danchin & Wagner, 1997; Velando & Freire, 2001).

Each model has a set of predictions that can be tested to see which distribution applies to a particular population of nesting birds. One of the predictions of the ideal free distribution, for example, is that if resources are patchy, high quality areas should contain a larger number of individuals than lower quality areas, as all individuals should have equal access to resources (Calsbeek & Sinervo, 2002). Support for the ideal despotic distribution, meanwhile, requires evidence that individuals breeding in suboptimal patches try to settle in optimal patches, and that such efforts are repelled via aggressive behaviour from the individuals in the favoured areas (Oro, 2008). Finally, the central-satellite model might be operating if newly built nests (typically belonging to young or poor quality pairs) are located adjacent to nests reoccupied from the previous breeding season, indicating a high quality nest site (Velando & Freire, 2001). Aside from these models, it is worth noting that other influences are also important in determining nest placement in gulls. Spatial distribution can be affected by tradition, for example, because of gulls' tendency towards philopatry and nest site fidelity (Bongiorno, 1970), while there might also be a genetic component to habitat selection (Rodway & Regehr, 1999).

Whatever the model describing the overall spatial distribution of nests in a colony, the results of several studies at a smaller scale illustrate the importance of nest density and neighbour interactions on breeding success. Territory size is plastic: it changes throughout the breeding cycle on both a short-term circadian basis and over longer time periods governed by key reproductive stages, such as chick rearing (Burger & Beer, 1975; Hunt & Hunt, 1975; Burger, 1980; Butler & Janes-Butler, 1982; Bukacińska &

Bukaciński, 1994). Various data suggest that a large territory is an asset, in that pairs occupying such spaces have a better reproductive success than pairs that are more confined (Hunt & Hunt, 1976a; Ewald *et al.*, 1980; Butler & Trivelpiece, 1981; but see Fetterolf, 1983a). Nest density, which is sometimes approximated by measuring the distance to nearest neighbours (e.g. Murphy *et al.*, 1992 Panov, 2009), necessarily affects the largest extent of the boundaries of a breeding territory, by determining the space available for each breeding pair. However, the implications of this scenario for a pair's reproductive success are tempered by the effects of density on predation, and by the possible operation of social interactions, such as conspecific attraction to, or competitive exclusion from, particular patches. The situation is further clouded by the effects of external factors, such as the availability of food, on density dependent nesting behaviour. In Western Gulls (*L. occidentalis*), for example, large territories improve reproductive success when food is scarce, probably because of the reduction in the risk of intraspecific predation, but there is no effect of territory size when food is plentiful (Hunt & Hunt, 1976a).

This complicated relationship might help explain why numerous studies examining the association between density on breeding success in gulls, and other seabirds, have produced conflicting results. Various authors have concluded that density has little or no effect on reproductive output (Patterson, 1965; Dexheimer & Southern, 1974; Hunt & Hunt, 1975; Jehl, 1994; Barbour *et al.*, 2000; Antolos *et al.*, 2006). Others have found a negative correlation between breeding success and density (Butler & Trivelpiece, 1981; Fetterolf, 1984; Stokes & Boersma, 2000), while yet more have suggested that the opposite is true (Birkhead, 1977; Kilpi, 1995; Oro, 1996a; Good, 2002; García Borboroglu *et al.*, 2008). Finally, some studies have suggested that an intermediate nest density is best for optimal reproductive success (Parsons, 1976).

Some of these discrepancies could be explained by the quality of pairs in particular parts of the colony. Recruits, for example, may be attracted to high density areas due to the presence of conspecifics, but forced to nest in less preferred, and thus lower density, region until they are dominant enough to establish a territory in the desired area (Chabrzyk & Coulson, 1976; Coulson *et al.*, 1982). The inexperience of breeders in low density areas could therefore account for the low reproductive success observed. Other factors, for instance Allee effects, whereby breeding success peaks at medium population densities due to the disadvantages of breeding at high (e.g. increased competition for resources) and low (e.g. decreased group defence against predators) densities, might also help determine density-mediated breeding success in colonies (Greene & Stamps, 2001; Oro *et al.*, 2006).

Alternatively, factors related to, but distinguishable from, density could be involved. In Great Black-backed Gulls (*L. marinus*), for example, breeding success is inversely related to the number of contiguous territories surrounding a pair's breeding site (Butler & Trivelpiece, 1981), which may be due to the fact that neighbours are often the most common predators of a nest (Gillett *et al.*, 1975; Davis & Dunn, 1976).

2.1.4 Reproductive success and breeder quality in gull colonies

The asymmetries in phenotypic quality found in individual gulls within breeding colonies translate into differences in reproductive success. Gulls breeding in sub-optimal habitats have been found to lay smaller clutches than pairs nesting in better areas (Montevecchi, 1978; Pierotti, 1987; Bosch & Sol, 1998; Lee *et al.*, 2008). In most species of gull, the modal clutch size is three eggs, although some pairs produce clutches of two, or lay only a single egg (section 3.1.2.1). While this intuitively affects reproductive success through the limit it places on the number of chicks produced, it has also been found that eggs from smaller clutches are less likely to hatch than those from larger clutches (Paynter, 1949; Harris, 1964; Brown, 1967b).

Gulls nesting in sub-optimal areas also tend to breed later in the season than those in better patches. The effect of laying date on reproductive success is more complicated than that of clutch size, although the two are inter-related, such that earlier laid clutches are bigger than those produced later in the season (Davis & Dunn, 1976; Kilpi, 1990; but see García Borboroglu *et al.*, 2008). Seasonal declines in hatching and fledging success (Brown, 1967b; Davis & Dunn, 1975; Parsons, 1976; García Borboroglu *et al.*, 2008) and egg volume, which is related to chick survival (Parsons, 1970; Lundberg & Väisänen, 1979; Bolton, 1991), have also been observed (Parsons, 1972; Davis & Dunn, 1976). All these factors thus contribute to the general reduction in breeding success with advancing laying date observed in many species (Paynter, 1949; Brown, 1967b; Kadlec & Drury, 1968; Burger, 1979). There is also some evidence that later hatching chicks have lower post-fledging survival than those hatched and fledged earlier in the season (Parsons *et al.*, 1976).

The causes of these trends are not entirely clear. There is some evidence that they are dependent on food availability, such that in those years when the normal food supply is disrupted, the usual relationship between time of breeding and reproductive success is in turn affected (Brouwer *et al.*, 1995; Rodway & Regehr, 1999; Mills *et al.*, 2008; Tomita *et al.*, 2009). Food availability has also been shown to affect egg volume, clutch size, and both hatching and fledging success, as well as the likelihood and age of recruitment (Mills *et al.*, 2008; Tomita *et al.*, 2009; Vieyra *et al.*, 2009). These associations may be mediated by the nutritional constraints of egg production (Houston *et al.*, 1983; Bolton *et al.*, 1992) as well as the energetic needs of the chicks (Pierotti & Annett, 1987; Annett & Pierotti, 1999). It is also known that hungry chicks are more likely to wander into neighbouring territories than well fed chicks, where they may die as a result of territorial aggression (Hunt & McLoon, 1975; Fetterolf, 1983a).

Seasonal affects on reproductive success could also be governed by the synchronicity of breeding. As discussed, the synchronization of reproductive behaviour helps to curtail egg and chick losses through predation, such that birds that breed at or shortly before the peak of the season, in terms of the activity of other members of the colony, achieve the highest breeding success

(Paynter, 1949; Patterson, 1965; Brown, 1967b; Kadlec & Drury, 1968; Parsons, 1975a; Davis & Dunn, 1976; Sydeman *et al.*, 1991; but see Hunt & Hunt, 1975). Increasing intraspecific cannibalism and general aggression towards chicks as the season advances have been found (Hunt & Hunt, 1976a; Spaans *et al.*, 1987), as well as evidence that escalating egg losses are due to theft by failed breeders (Davis & Dunn, 1976), bringing about negative feedback on reproductive success towards the end of the breeding season. However, the seasonal patterns observed could also be related to fluctuations in food availability.

Some authors have suggested that once all other effects are controlled for, the best predictor of reproductive success is an individual's age (Pugesek & Diem, 1983). Clutch size and egg volume are bigger in older birds than in younger breeders (Coulson, 1966; Mills, 1973; Ryder, 1975; Chabrzyk & Coulson, 1976; Coulson *et al.*, 1982; Pugesek & Diem, 1983; Reid, 1988; Pyle *et al.*, 1991; Sydeman *et al.*, 1991; Vieyra *et al.*, 2009), with the latter increasing to a plateau at eight to ten years old in most species, before beginning to decline in an individual's mid-teens (Davis, 1975a; Mills, 1979; Coulson *et al.*, 1982; Reid, 1988; Sydeman & Emslie, 1992; Vieyra *et al.*, 2009). Fledging and hatching success also improve with age (Coulson, 1966; Chabrzyk & Coulson, 1976; Pugesek, 1987; Reid, 1988; Pugesek & Diem, 1990; Pyle *et al.*, 1991; Aubry *et al.*, 2009; Vieyra *et al.*, 2009). These parameters are correlated with laying date, since older pairs reproduce earlier in the breeding season than young birds (Coulson, 1966; Mills, 1973; Parsons, 1975b; Ryder, 1975; Reid, 1988; Sydeman *et al.*, 1991). However, the timing of breeding is thought to be partly genetically determined, such that it is constrained by an individual's intrinsic quality despite modifications with age (Brommer *et al.*, 2008; Brommer & Rattiste, 2008). Older pairs are thought to raise their breeding performance through increased reproductive effort, as the knock-on effect of elevated mortality becomes less important with advancing age (Pugesek, 1983; 1987; but see Reid, 1988). Reproductive success is also informed by breeding experience (Coulson, 1966; Aubry *et al.*, 2009), such that older parents are better able to effectively incubate, nourish and defend their brood, and coordinate parental care duties with their partners (Reid, 1988; Sydeman *et al.*, 1991).

2.2 RESEARCH THEMES

Models were fitted to look for associations between reproductive success and the various aspects of breeding biology evaluated in a colony of Lesser Black-backed Gulls. The nesting behaviour of this species was studied as part of a wider research project on the mechanisms governing begging and feeding behaviour in young chicks (Chapters 3, 4 and 5). Much of the work described in this chapter arose as a result of attempts to characterize the possible influences of factors determined during nesting (e.g. laying date, egg size) on this chick behaviour (section 3.1.2.1). Breeding was therefore tracked from egg laying through to hatching. The resulting data contained many correlates of reproductive success, namely egg volume, clutch size and hatching success, which are assessed in this chapter. The work in Chapters 3, 4 and 5 also required chicks of known age and experience to elucidate how this behaviour develops post-hatching (section 3.1.2.2), which brought about the experimental technique described in sections 2.3.2 and 2.4.2. The consequent information on the phenotype of hatchlings was thus also available for modelling parental reproductive success; hatchling phenotype is an important influence on this, as robust chicks are more likely to fledge, recruit and eventually breed themselves than feeble ones.

2.2.1 Flat Holm Island and its gulls

All work in this chapter was carried out between early April and late June of 2007 and 2008 on Flat Holm (51°23' N, 3°07' W), a small island (32 ha at high tide, and up to 52 ha at low tide) in the mouth of the Severn Estuary, approximately 8 km south of Cardiff (Fig. 2.4). As its name suggests, Flat Holm's elevation above mean sea level is low. The island slopes out of the sea on the western side and rises to a high point of 32 m OSD near the lighthouse on the south-eastern point of the island. The island is composed of

Carboniferous limestone, with cliffs around the south and east of the island, giving way to rocky shores and shingle beaches towards the north and west.

Fig 2.4. A 1:200,000 map of the inner Bristol Channel, showing Flat Holm Island. © Ordnance Survey/EDINA Digimap, 2005.

Archaeological excavations have revealed that Flat Holm has been occupied by man for thousands of years, with the oldest known remains dating from the Bronze Age. It was also farmed from the Medieval Period to the mid-twentieth century. Today, the only human inhabitants of the island are wardens and volunteers employed by the Flat Holm Project, which manages the island as a Local Nature Reserve on behalf of Cardiff City Council. Since 1986, the northern area of the island has been grazed by sheep and goats, and vegetation mowed to preserve and encourage maritime grassland, for which the island has Site of Special Scientific Interest (SSSI) status. The species found here include Buckshorn Plantain (*Plantago coronopus*), Sea Storks Bill (*Erodium maritimum*) and Thrift (*Armeria maritima*). The rest of the island is left wild, with the exception of a number of paths which are kept clear of vegetation. Plants growing on this part of the island include the Common Nettle (*Urtica dioica*), Elder (*Sambucus nigra*), Bracken (*Pteridium aquilinum*), Bramble (*Rubus fruticosus*) and Wild Turnip (*Brassica rapa*). It is on this "unmanaged" side of the island, and around the cliffs and shores, that gulls nest.[8]

Flat Holm is home to an important breeding colony of Lesser Black-backed Gulls, representing approximately 3% of the British population of this species (Mitchell *et al.*, 2004). This feature is therefore also listed in the SSSI citation. The Lesser Black-backed Gulls of Flat Holm are well suited to study, as their nests are easily accessible. The gullery also receives a sizeable number of human visitors. Consequently, the birds are relatively habituated to human presence and hence less sensitive to investigator disturbance than gulls at more rarely visited colonies (Martínez-Abraín *et al.*, 2008). Flat Holm's Lesser Black-backed Gulls have been the subject of research since the 1970s. Notable studies include those of Greg Mudge and Peter Ferns (Cardiff University), who investigated feeding ecology, and Mark Bolton (Glasgow University) and Andy Stanworth (Cardiff University), who both (independently) examined egg production.

The first record of gulls breeding on Flat Holm dates from 1954, when five Herring Gull (*L. argentatus*) nests were found. These birds were presumed to have colonized Flat Holm from the neighbouring isle of Steep Holm, which is thought to have hosted breeding gulls since the eighteenth century (Mudge, 1978). Lesser Black-backed Gulls were first reported on Flat Holm in 1957. Regular censuses of Flat Holm's breeding gulls took place between 1954 and 1980. Since 1983, a rigorous annual count has been carried out, the details of

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[8] Gulls attempting to nest on the maritime grassland part of the island have their eggs and nests removed, as it is thought that the behaviour of breeding gulls (i.e. grass-pulling) and their faeces have detrimental effects on this type of vegetation. Flat Holm's management is hence partly a balance of the two features (the gulls and the maritime grassland) which comprise the SSSI.

which can be found in Ferns and Mudge (1981). In common with many gull populations around the world (e.g. Kadlec & Drury, 1968; Spaans, 1971; Mudge, 1978), numbers of both Herring and Lesser Black-backed Gulls rose steeply on Flat Holm between the 1950s and the 1970s, reaching more than 4000 breeding pairs of each species by 1974 (Mudge, 1978). However, with the advent of botulism, and the onset of island management, the gull population on Flat Holm is now maintained at a lower level. The number of Herring Gulls has also dramatically declined relative to the number of Lesser Black-backed Gulls. In 2007 and 2008, there were 3732 and 4197 pairs of Lesser Black-backed Gulls on Flat Holm respectively, but only around 400 breeding pairs of Herring Gulls. The Lesser Black-backed Gulls currently largely inhabit the top of the island, with the Herring Gulls mostly confined to the cliffs. Great Black-backed Gulls (*L. marinus*) have also nested on Flat Holm since 1962 (Mudge, 1978), but numbers have remained stable at one to two breeding pairs, which occupy prominent cliff nest sites.

As well as gulls, other vertebrate fauna on Flat Holm include Rabbits (*Oryctolagus cuniculus*), Shelduck (*Tadorna tadorna*), Oystercatchers (*Haematopus ostralegus*), Slow Worms (*Anguis fragilis*), Common Lizards (*Lacerta vivipara*) and several passerine birds. The island is also visited by hunting Buzzards (*Buteo buteo*), Peregrine Falcons (*Falco peregrinus*) and Merlins (*Falco columbarius*), which cause widespread alarm in the gull colony.

2.3 METHODS

The 2007 field season commenced on 2nd April and finished on 25th June, while in 2008 work began on 3rd April and ran until 26th June. These stints on Flat Holm encompassed almost the entire Lesser Black-backed Gull laying period, with a small number of late eggs still appearing at the end of each season, but mostly as a result of re-laying following earlier breeding failure. The majority of hatching was also witnessed. Work was carried out under licences OTH:SB:02:2007/2008 from the Countryside Council for Wales, and complied with the Association for the Study of Animal Behaviour's guidelines on the ethical treatment of animals in behavioural research.

2.3.1 Assessment of nesting behaviour

During 2006, young chicks were removed from nests throughout the island for behavioural tests (section 3.3.1.1). This required daily searches for chicks of a suitable age, during which it was noted, as has been found elsewhere (e.g. Pierotti, 1982), that chicks from different habitats hatched at different times in the breeding season, and that the nests in these areas appeared to share particular attributes in terms of, for example, the quantity of nesting material used. In 2007 and 2008, it was thus decided to select all chicks from a closely monitored area of the colony that encompassed several habitats, to maximise the likelihood of obtaining sufficient numbers of chicks throughout the hatching season and to minimize search time as nest location would be known, and egg hatching date could be predicted. This method also allowed the assessment of factors that could influence chick phenotype, such as laying order and egg size (section 3.1.2.1), and the evaluation of parental nesting behaviour. Tests could therefore be carried out to see whether any of these variables predicted chick behaviour in the experiments described in Chapters 3, 4 and 5.

The area chosen for monitoring was towards the centre of the south-western part of the gull colony (Figs. 2.5 and 2.6), and included a range of nesting habitats from those in open, rocky sites with no vegetation to all, to nests in densely vegetated areas where they were almost completely concealed. The principal vegetation in the monitored region was grass, Bracken, Wild Turnip (in 2007 only, but not in 2008 as this is a biennial plant), Common Nettles, Brambles and Elder. The size of the area studied was 7700 m^2, (110 m x 70 m) divided into a 10 m by 10 m grid with flagged bamboo canes, which were erected each year at the start of the field season (Fig. 2.7).

Fig. 2.5. An aerial view of Flat Holm. The region of the gull colony monitored in this study is shown in red. The division of the island between the managed side to the north, where only grassland persists, and the unmanaged side, to the south where thicker vegetation grows, can also be seen.

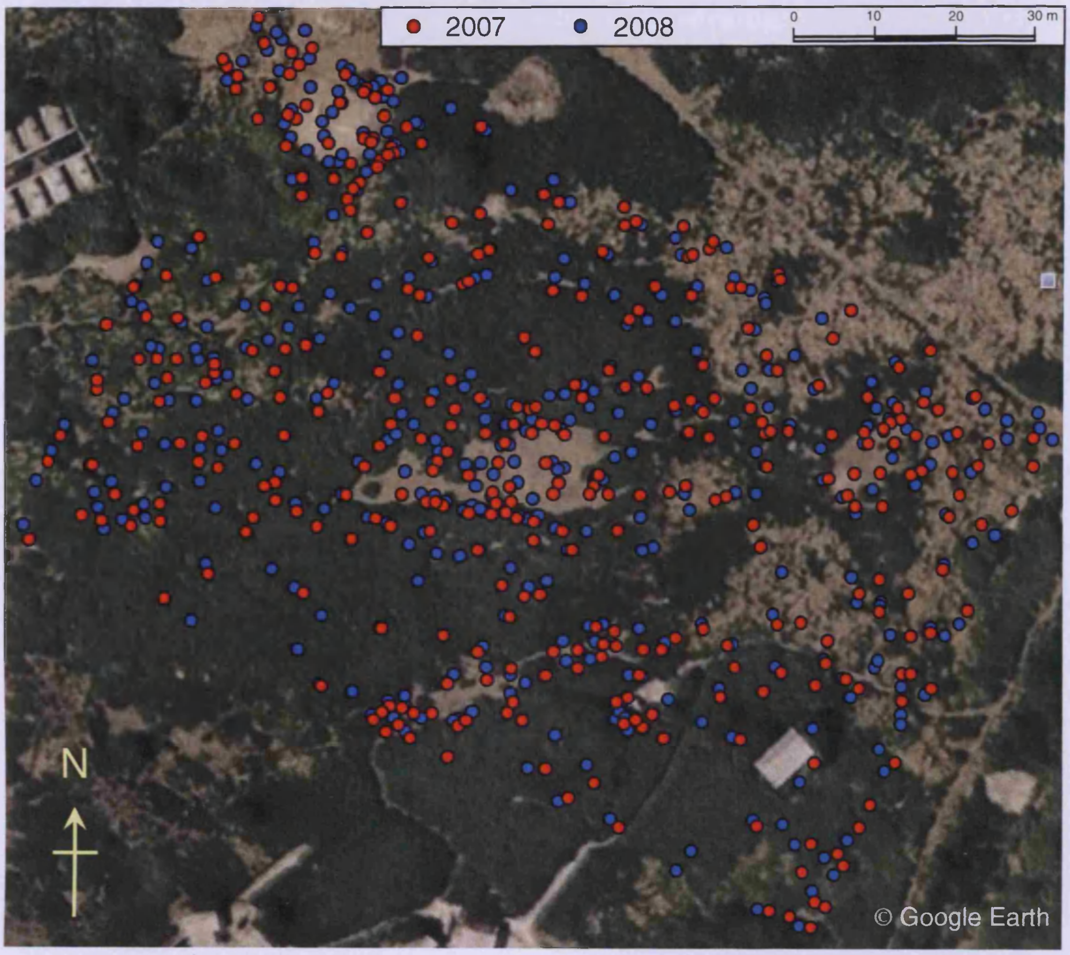

Fig. 2.6. The distribution of nests monitored in 2007 and 2008. The north-east corner of the study area corresponds to the origin of the axes in Figs. 2.17 and 2.18.

Fig. 2.7. Lesser Blacked-backed Gulls next to flag G5 on Flat Holm, April 2008. These individuals were nesting in an open, gassy area, but to the background (where flags H5 and I5 are visible), nettles and scrub can be seen, in which nests were also located.

This grid was walked systematically on a daily basis[9] to check for nesting activity, moving slowly through the colony along the same route each time to minimize disturbance to the breeding birds (Robert & Ralph, 1975; Fetterolf, 1983b; Brown & Morris, 1995; Martínez-Abraín *et al.*, 2008). Any eggs found were measured with a digital calliper to the nearest 0.01 mm, and marked with the letter A, B, or C (to denote first, second and third laid eggs respectively) in indelible, non-toxic ink. Egg volume (cm^3) was calculated as length (mm) x breadth (mm) x 0.000476 (Harris, 1964). Laying date was also noted, along with the angular extent of vegetation over 10 cm high surrounding and contiguous with the nest at the time of clutch completion. For analytical purposes, the latter was placed into six discrete categories (0° - 59°, 60° - 119°, 120° – 179°, 180° – 239°, 240° – 299°, 300° - 360°). In 2008 only, nest quality was estimated by subjectively placing nests on a five point scale based on nest appearance (Fig. 2.8). This was again recorded at clutch completion, as nests were often improved through the addition of extra

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[9] Days were occasionally missed due to bad weather.

nesting material during the laying period. Clutch size was counted as the number of eggs produced per breeding attempt, such that records were not altered if an egg was lost. If a clutch was re-laid following previous breeding failure, this was considered a separate breeding attempt by the pair concerned, and the replacement eggs were counted again as A, B or C. Finally, every nest with eggs was recorded by a Cartesian coordinate system within the grid, such that each one could be easily relocated and nearest neighbour distance calculated.

Fig. 2.8. Examples of nests on the five point classification scale. The letters used to denote laying order are also visible in these photos. (a) Good, (b) Good-Moderate, (c) Moderate, (d) Moderate-Poor, (e) Poor. There was generally a progressive reduction in the amount of nesting material supporting the eggs, and the organization of the nest into a well-rounded, symmetrical nest-cup, between Good and Poor nests.

2.3.2 Chick selection and care

The primary reason that the monitoring of nesting behaviour was started was in order to obtain chicks for behavioural experiments. It was imperative that these chicks were kept as naïve as possible to all stimuli associated with the pecking response and feeding, as the innate forms of these behaviours were to be studied (Chapters 3, 4 and 5). The best way to do this would be to remove eggs after laying and hatch them in an incubator in a laboratory environment, where all external stimulation could be carefully controlled. However, this was not possible on Flat Holm, and is generally not feasible under field conditions. Indeed, conventional incubators could not be used, as even though Flat Holm has a limited electricity supply and a portable generator was purchased for this work, there was not enough power available to run the number of incubators required to incubate enough eggs over the entire the incubation period, in order to provide a sufficient number of chicks for the behavioural experiments. Instead, a technique was developed that involved removing eggs for hatching shortly before the end of incubation, using simple makeshift incubators. This left the parents in charge of the majority of incubation, thus eliminating the need for the rigorous control of egg temperature, humidity and rotation. The method described is similar to that employed by other researchers (e.g. Cullen, 1962; Quine & Cullen, 1964), but these authors did not provide information of the conditions used, or the hatching success rates compared to chicks in the wild.

Eggs for experimental hatching were taken from the monitored area of the gull colony once external pipping had taken place, such that the chicks within had pecked a small hole in the egg shell to reveal the beak with the egg tooth attached (Fig. 2.9a), and vocalizations were clearly audible. Eggs were selected on the basis of predicted hatching date and laying order, so as to provide an equal proportion of A, B and C eggs. No more than one egg per nest was removed to avoid pseudoreplication of chicks within nests (Hurlbert, 1984), and attempts were made to only take eggs from nests with a clutch size of three, although in 15 cases (seven in 2007, eight in 2008) eggs originated from clutches of two. A total of 91 eggs were selected for hatching between 21st May and 16th June in 2007, while 121 eggs were removed between 19th May and 13th June in 2008.

As well as dispensing with the need for conventional incubators, taking eggs at the pipping stage had another advantage. Parents and offspring begin communicating acoustically before chick hatching. Chicks start to recognize their parents' vocalizations before hatching, and alter their pecking behaviour, vocalizations and posture when exposed to certain parental calls post-hatching (Impekoven, 1970; 1976). The peeping calls chicks emit whilst still in the egg can also provoke behavioural responses from their parents (Impekoven, 1973; Evans *et al.*, 1994). It was therefore considered that such prenatal acoustic contact between parents and late-stage eggs in the colony might aid parent-offspring recognition and thus facilitate the successful return of chicks to the nest following behavioural testing. Removing eggs just before hatching also obviated the need to replace them with dummy eggs, as females do not re-lay single eggs lost at this time (personal observation).

Pipped eggs were carefully transported from the colony in individual, numbered bird bags. Up to 15 eggs were taken at once, a procedure which took approximately 20 minutes. These eggs were kept in an unheated room of the abandoned fog horn keeper's cottage on Flat Holm. They were housed individually in adjacent compartments (8.5 cm long x 8.5 cm wide x 30.5 cm high) in a cardboard box. Pipped eggs were thus in acoustic contact with their neighbours, which has been shown to promote hatching synchrony in laboratory experiments (Schwagmeyer *et al.*, 1991) and was hence thought to facilitate having all chicks ready for testing at once. Each compartment had air holes punched through the sides, and was lined with straw, newspaper and absorbent kitchen towel, which raised the eggs by about 10 cm from the bottom of the box. The box was placed on insulating fibreboard, and heated from below by a 24 W heat mat (Exo Terra Vivarium Heater), and from above by two 100 W infrared heat lamps (Exo Terra Heat Glo). The temperature of the box was maintained at approximately 35°C, by adjusting the distance between the lamps and the box at different times of the day. This temperature was based on that reported for gull eggs in the wild (Lee *et al.*, 1993; Evans *et al*, 1995; Niizuma *et al.*, 2005). The box was covered with a towel, which was sprayed regularly with a fine mist to maintain higher than ambient relative humidity (Ar & Sidis, 2002). Power was supplied by a Kipor (KDE 6700 TA) 4.5 KVA portable diesel generator and a 95 AH, 12 V battery (the generator could not be run continuously, so once charged from the generator, the battery was used for approximately three hours in every twelve).

Eggs were placed in the box such that the chicks' pipping holes faced upwards. They were not turned, but were instead simply left alone to hatch, subject to regular inspections to ensure they were not becoming too hot or cold (they were kept warm to the touch). Eggs were checked on an hourly basis during the day, and every three hours at night. Most eggs hatched within 24 hours of collection. Upon hatching, all egg shell was removed from the chick's compartment and the chick left to dry out, after which time a short length of electrical insulation tape was placed on the left tarsus, labelled with its parental nest coordinates and laying order.

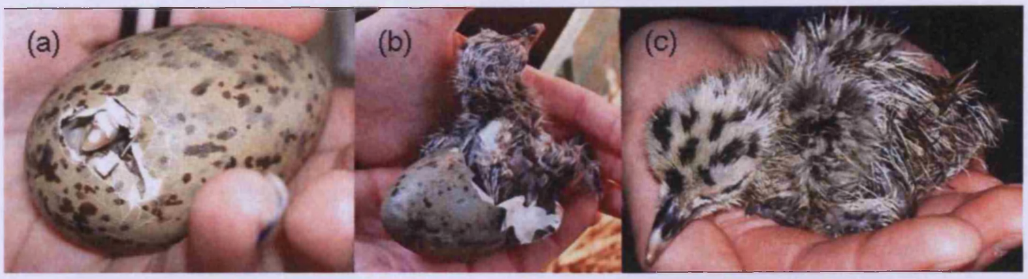

Fig. 2.9. The experimental hatching of Lesser Black-backed Gull chicks. (a) pipped egg collected from the gullery, (b) newly hatched chick with its eggshell, (c) chick beginning to dry out approximately one hour after hatching.

Prior to experimentation chicks were given water from a transparent plastic 0.1 ml syringe, which contained small quantities of sugar solution if they appeared weak, but were not fed. Chicks in the wild are not fed until several hours after hatching (Tinbergen & Perdeck, 1950), during which time they draw energy from their yolk sac reserves, which are not depleted until four days post-hatching (Hario *et al.*, 2004). As well as maintaining chicks' naivety to pecking stimuli, depriving the chicks of food before experiments ensured they were motivated to peck, as sated chicks show lower levels of begging behaviour (Impekoven, 1969; Iacovides & Evans 1998).

Mean chick age at the start of experimentation was 34.2 hours in 2007, with a range of 14.0 to 48.0 hours. In 2008, mean age was 25.8 hours, with a range of 3.8 to 48.3 hours. Chicks were tested once they appeared strong enough to walk around and coordinate themselves sufficiently well to successfully peck at a stimulus. Any chick that was too feeble was not tested, but was instead provided with food and water and returned to the nest. As chicks had been kept in isolation and were not fed, none had been exposed to stimuli normally associated with the pecking response before testing, and as such any behaviour observed should have been innate.

Following experimentation, chicks were placed together in an open straw-lined pen (54 cm long x 37 cm wide x 23 cm high), heated from above by two 100 W infrared heat lamps (Exo Terra Heat Glo), which kept the temperate between 23°C and 27°C, an ambient range over which young chicks can maintain their homoeothermic body temperature (Dunn, 1976). Each chick was weighed and measured, and then fed to satiation on a mixture of fish-based tinned cat food and tinned tuna. These tested chicks were then returned to their parental nest, either directly after feeding, or the following day if tests were carried out in the evening, or if weather conditions were bad. If chicks were kept for an additional period, they were fed and watered every three hours. Tarsus labels were removed before chicks were placed back in the nest. Most chicks were approximately two days old when they were returned to their parents. No chick was older than three days.

Fig. 2.10. Chicks awaiting measurement, following participation in behavioural tests, May 2008.

Observations of nests after the return of chicks indicated that although some appeared disorientated at first, they were readily accepted back by their parents, and normal family interactions ensued. This might have been the case even had precautions not been taken to allow pre-hatching parent-offspring vocal communication, and the careful matching of chicks to the correct parental nest, as studies have shown that a parent's recognition of its own young is not precise during the first days of a chick's life (Miller & Emlen, 1975; Knudsen & Evans, 1986; Galusha & Carter, 1987). In fact, adoption of small foreign chicks during this time is not uncommon among several species of gull (Tinbergen, 1953; Holley, 1981; Pierotti & Murphy, 1987; Brown, 1998; Bukaciński *et al.*, 2000).

2.3.3 Statistical treatment

Results were analyzed in R version 2.8.1 (R Core Development Team, 2008), with the use of additional packages "nlme" (Pinheiro *et al.*, 2008), "lme4" (Bates *et al.*, 2008), "multcomp" (Hothorn *et al.*, 2008), "MASS" (Venables & Ripley, 2002) and "spatstat" (Baddeley & Turner, 2005). Graphical figures were prepared in R version 2.8.1 (R Core Development Team, 2008) and ArcMap 9.2 (ESRI, 2006). Statistical tests were two-tailed, with a significance level of 0.05. All values are given as arithmetic mean ± S.E.

Three main classes of model were fitted to examine the indicators of reproductive success measured. Egg volume was assessed with linear mixed-effects models (LMMs) (Pinheiro & Bates, 2000) using the "nlme" package, with the nest of origin included as a random factor. In these models, eggs for which the volume was not known (eight in 2007, four in 2008), normally because they were broken or had disappeared before measurement was possible, were excluded. Factors influencing clutch size were evaluated with general linearized models (GLMs) with a Poisson error (Crawley, 2007). Generalized linear mixed models (GLMMs) (Bolker *et al.*, 2009) with a binomial error were fitted using the "lme4" package, to investigate variables governing the likelihood that eggs hatched, with the identity of the nest from which the eggs originated again fitted as a random factor. The response variable was binary, with a code of 0 if an egg did not hatch, and 1 if an egg did. Eggs of unknown fate were excluded from the analysis, such that models included 873 of the 950 eggs recorded in 2007, and 948 of the 1011 eggs tracked in 2008. A similar method was used to examine the eggs that did not hatch, using a binary response variable for those that disappeared from the nest before incubation was complete, and those that remained in the nest unhatched.

Explanatory variables in all models were the amount of vegetation around the nest, nest quality (2008 only), laying date (subdivided into the week since the start of the laying season in the monitored area),[10] year, and the distance to the nearest nest, calculated by Euclidian geometry with the "spatstat" package. Egg volume and clutch size were fitted as explanatory variables in the models where they were not the response variable. Egg laying order was included as a categorical variable in the models of egg volume and hatching success.

In all models, interactions were only fitted if they were thought to be informative and biologically meaningful to help reduce the problem of multiplicity of p-values (Grafen & Hails, 2002). Therefore, no interactions of a higher order than two-way were included. Model simplification proceeded via stepwise deletion of non-significant terms (Crawley, 2007), with comparison of the p-value of the likelihood ratio statistic and the Aikaike Information Criterion (AIC) at each step (Pinheiro & Bates, 2000).[11] *Post-hoc* multiple pairwise comparisons of the different levels of significant categorical explanatory variables were undertaken with the "multcomp" package.

The distribution of nests in the colony in each year was tested to see if it differed from complete spatial randomness (CSR). This was done by comparing the distribution of nests within each 100 m^2 square of the grid

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[10] 10th April was taken as the start of week one in both years, even though eggs were not found until a little later in 2007, so that laying could be compared over the same calendar period.

[11] In cases where a variable approached significance, it was retained in the model if its exclusion brought about a significant likelihood ratio statistic and an increased AIC value.

with that predicted by a Poisson distribution using the χ^2 test (Crawley, 2007).

A comparison was made of the hatching success of eggs subject to the experimental technique and those hatched in the field for the 2008 breeding season only, as insufficient field data were collected in 2007. The χ^2 test was used to compare the proportion of chicks that failed to hatch using the experimental technique with that of (a) the total number of eggs that pipped in the colony, (b) pipped eggs from unmanipulated nests only, where no eggs were removed for experimental hatching (c) pipped eggs from clutches of two and three (for manipulated and unmanipulated nests), as the eggs taken always came from clutches of this size. Eggs in the field that pipped before 19th May or after 13th June (41 eggs) were excluded from the analysis, so that hatching under experimental and field conditions was assessed over the same time period. Eggs were also omitted if their hatching could not be ascertained (69 eggs), either because they disappeared at around their predicted hatching date with no evidence of hatching, or because fieldwork finished before they were due to hatch. Nine eggs (eight from unmanipulated nests) were also excluded because their pipping was recorded, but their fate after that was not known.

2.4 RESULTS

2.4.1 Nesting behaviour

In both 2007 and 2008, laying in the study grid commenced slightly after the very first eggs were found on Flat Holm, with the first egg on the island discovered on 9th April in 2007, but no laying in the grid until around 13th April.[12] There was a delay of six days between the colony's first egg on 4th April 2008, and the beginning of laying in the grid on 10th April. However,

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[12] Five eggs were found on 15th April 2007, including two in the same nest. Thus, some of these were certainly laid before 15th, although the exact date was not known as the grid was still being constructed prior to 15th and proper monitoring was not yet in progress.

very few eggs were found on the island at the start of each breeding season, such that nesting activity in the study area was quite typical of that in the colony as a whole. In total, 950 eggs in 348 nests were tracked within the grid in 2007. There was slightly more nesting activity in 2008, with 1011 eggs in 366 nests (Fig. 2.11). In 2007, two of the nests tracked belonged to Herring Gulls, and one to a mixed pair where the male was a Herring Gull and the female a Lesser Black-backed Gull. By 2008 one of the Herring Gull pairs had gone. In 2007, the first chicks were found on 15th May, although some of these almost certainly hatched before this date, as no monitoring was possible between 11th and 14th May (inclusive) due to bad weather. The first chick in 2008 hatched on 13th May. In each year, egg production in the monitored area peaked in the fourth week after the first egg was found (Fig. 2.11), and chick hatching peaked in the eighth week. These peaks were more pronounced in 2008 than in 2007.

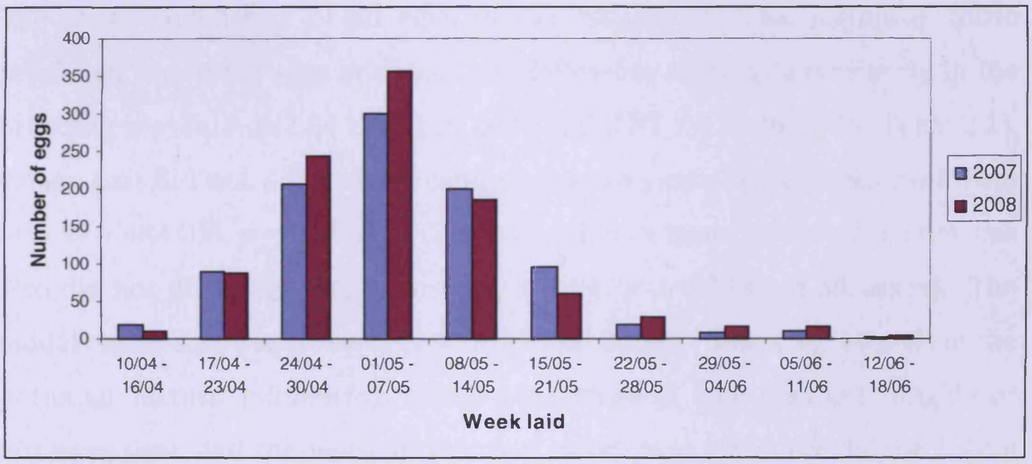

Fig. 2.11. Seasonal variation in egg production in 2007 and 2008.

At the beginning of each field season, several nests were already present in the monitored area, but many more appeared during the egg production period. In accordance with other studies (Tinbergen, 1953; Harper, 1971), some of these nests were never used, but instead appeared to be "practice" nests that a pair built adjacent to the one they eventually settled in, although it is also possible that they belonged to birds that were later displaced from the breeding territory. Some nests were built several days before egg production commenced, while others were rapidly constructed immediately prior to laying. Nesting material, if present, normally consisted of grass, small sticks and sometimes mud. Other objects including chicken bones, wool (shed by the island's Soay sheep) and pieces of plastic refuse were also frequently present. Improvement of the nest, in terms of the addition of nesting materials, continued while the clutch was laid, and sometimes throughout the incubation period, a behaviour similar to that reported for other species (Beer, 1963; 1965). Eggs were normally laid every other day, although a gap of two days was frequently seen between the production of the B and C egg in a clutch of three. Considering only those eggs for which both laying and hatching dates were certain, incubation time was 28.34 ± 0.06 days for A eggs (2007, n = 162; 2008, n = 204), 26.58 ± 0.05 days for B eggs (2007, n = 155; 2008, n = 225), and 25.69 ± 0.05 days for C eggs (2007, n = 111; 2008, n = 179). Overall incubation time was 26.95 ± 0.05 days.

The mean clutch size of all eggs in the monitored area, including those produced to replace eggs or chicks lost following nesting failure early in the breeding season, was 2.84 ± 0.01 in 2007 and 2.82 ± 0.01 in 2008 (Table 2.1), values that did not differ significantly between years (Wilcoxon's rank sum test, W = 484406, $p = 0.4667$). The proportion of nests with each clutch size also did not differ between years ($\chi^2_1 \leq 0.04$, $p \geq 0.8332$ in all cases). The modal clutch size was three eggs in 2007 and 2008 (Table 2.1). Models of the potential factors influencing clutch size showed that nearest neighbour distance, year and the week in which a clutch was produced in the laying season had no significant effect. There was a trend towards a reduction in clutch size with decreasing vegetation cover around the nest, with contrasts showing that nests encircled by more than 240° cover had larger clutches than those with less than 60° cover (GLM, $z \geq 2.05$, $p \leq 0.0440$ in all cases), although comparison of the deviance of models with and without this factor retained showed a non-significant effect of eliminating it ($\chi^2_5 = 8.40$, $p = 0.136$). The same minimum adequate model was found when only the 2008 data was considered, so that nest quality could be assessed. Again, contrasts showed a significant drop in clutch size between Good and Poor nests (GLM, z

= -2.04, $p = 0.0412$), but there was no significant effect of nest quality overall, as seen through comparison of deviance when it had been deleted from the model ($\chi^2_4 = 5.64$, $p = 0.228$).

Year	Clutch size	No. nests	Egg volume (cm^3)*
2007	1	25 (7.2%)	A = 67.82 ± 1.25
	2	56 (16.1%)	A = 69.70 ± 0.87, B = 65.04 ± 0.97
	3	266 (76.4%)	A = 71.61 ± 0.47, B = 69.27 ± 0.48, C = 63.45 ± 0.43
	4	1 (0.3%)	
	Total	*348*	
2008	1	24 (6.6%)	A = 68.09 ± 1.53
	2	61 (16.7%)	A = 68.68 ± 0.92, B = 64.25 ± 0.99
	3	280 (76.5%)	A = 71.70 ± 0.36, B = 70.24 ± 0.36, C = 64.95 ± 0.36
	4	1 (0.3%)	
	Total	*366*	

Table 2.1. Clutch sizes and egg volumes for first clutches. * - figures apply to nests containing all eggs of known volume and laying order only (262 nests in 2007, 353 nests in 2008).

Mean egg volume for all eggs recorded in the monitored area was 67.89 ± 0.23 cm^3 in 2007 and 68.48 ± 0.21 cm^3 in 2008 (Table 2.1). These figures were not significantly different (LMM, $F_{1,1248} = 2.14$, $p = 0.1438$). Egg volume was also not predicted by clutch size, the amount of vegetation around the nest, or the distance to the nearest neighbour. However, there was a significant week on week decline in egg volume over the course of the laying season in both 2007 and 2008 (LMM, $F_{9,1240} = 22.73$, $p < 0.0001$) (Fig. 2.12). A separate model including only eggs of known laying order, showed that the week in which an egg was laid was again a significant explanatory variable, along with laying order (LMM, $F_{2,1037} = 434.68$, $p < 0.0001$) (Fig. 2.13). *Post-hoc* tests revealed that this was due to a significant drop in egg volume between the A and B eggs and B and C eggs ($z \leq -10.88$, $p < 0.0001$). Analysis of the 2008 data only, to assess the effect of nest quality, revealed that this variable did have a significant relationship with egg volume (in addition to the egg laying order and date as seen in the model for both years) (LMM, $F_{4,358} = 2.50$, $p = 0.0421$). *Post-hoc* examination of this effect shows that egg volume in Poor and Moderate-Poor quality nests was smaller than that in Good nests ($z \leq -3.04$, $p \leq 0.0196$).

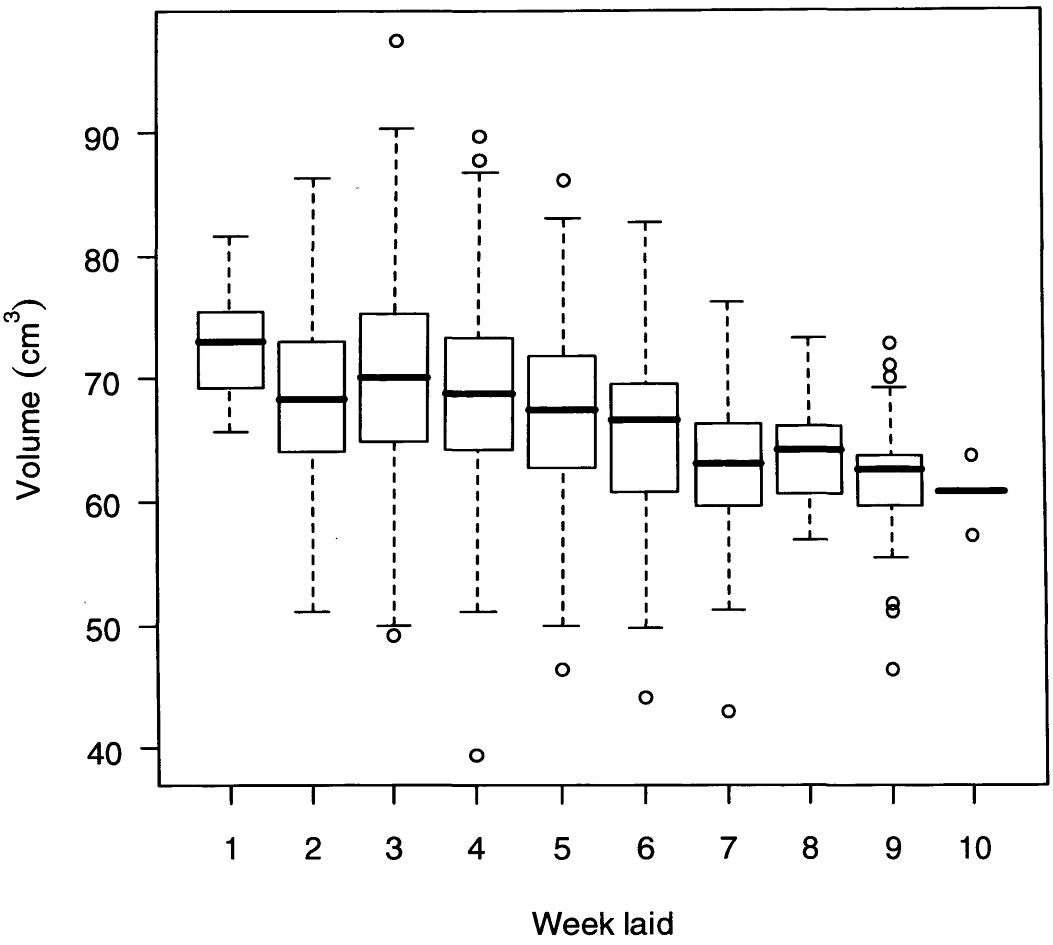

Fig. 2.12. The relationship between laying date and egg volume. There was a significant decrease in egg volume over the course of the breeding season. Data for 2007 and 2008 were pooled to obtain a single graph as there was no significant difference between the two years.[13]

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[13] In this boxplot and all henceforth: central bar in box – median, bottom of box – lower quartile, top of box – upper quartile, whiskers – maximum/minimum values or 1.5 times interquartile range (whichever is smaller), outliers – values exceeding 1.5 times interquartile range above third quartile and below first quartile.

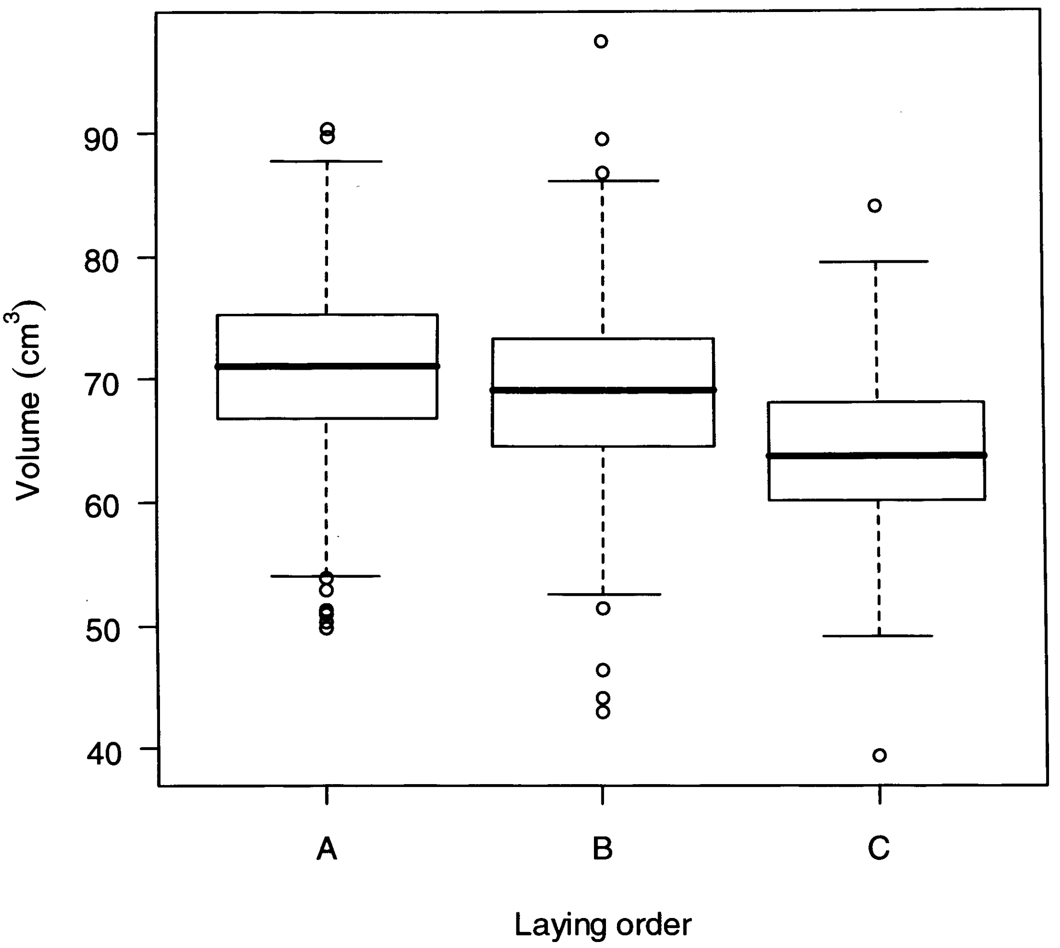

Fig. 2.13. Effect of laying order on egg volume. There is a significant decline as clutches are laid. Numbers pooled for 2007 and 2008 to obtain a single graph as there was no significant difference between years.

A further investigation of egg volume was carried out by fitting a model with only the volume of first laid (A) eggs as a response variable. Simplification again showed a significant decline in volume over the laying season (ANOVA, $F_{9,609} = 3.39$, $p = 0.0005$), but also an effect of clutch size (ANOVA, $F_{2,609} = 12.82$, $p < 0.0001$), with A eggs from three-egg clutches being significantly larger than those from two-egg or one-egg clutches ($t \geq 3.74$, $p \leq 0.0008$). There was also a significant interaction between the week in which an egg was laid and the size of the clutch from which it originated (ANOVA, $F_{16,609} = 2.00$, $p = 0.0113$), with the shape of the relationship between clutch size and seasonal decline in egg volume differing between one-egg clutches and clutches of two and three. However, this effect appears to be generated by the smaller sample size of single-egg clutches, and thus the influence of outliers. It is also worth noting that the overall effect of the relationship between the egg volume of A eggs and clutch size, laying date and their interaction is weak, with an adjusted R^2 of 8.78%.

In 2007, 64.7% of eggs in the monitored area were known to have hatched, compared to 65.7% of eggs in 2008. In 2007, 27.5% of eggs were known to have failed to hatch, while in 2008 this figure was 28.1%. The remaining eggs in each year (7.8% in 2007, 6.2% in 2008) were of unknown fate, either because the field season finished before they were due to hatch, or because they disappeared at approximately their due hatching date, but no evidence of hatching was found. These figures give a minimum estimate of 1.76 chicks hatched per nest in 2007, and 1.81 in 2008. Of the eggs in which hatching success could be ascertained, models revealed that the likelihood of hatching was significantly positively associated with increasing egg volume (GLMM, $z = 2.37$, $p = 0.0180$) and clutch size (GLMM, $z \geq 3.58$, $p \leq 0.0003$) (Fig. 2.14). This effect can be clearly appreciated through examination of the raw figures (combining numbers for 2007 and 2008 data as there was no significant year effect, and considering eggs of known fate only), which showed that 18.6% of eggs from single egg clutches hatched, against 56.0% of eggs from clutches of two, and 73.4% of eggs from a clutch size of three. Comparisons of the likelihood ratio showed that nest vegetation cover needed to be retained in the model ($\chi^2_5 = 13.78$, $p = 0.0171$). *Post-hoc* tests showed that eggs in nests surrounded by more than 240° vegetation were significantly more likely to hatch than those with less than 60° ($z \geq 3.11$, $p \leq 0.0204$). The week in which an egg was laid was also retained in the model ($\chi^2_8 = 31.13$, $p = 0.0001$), with multiple comparisons showing that eggs produced in the first four weeks of the laying season were equally likely to hatch, but those laid later suffered a significant drop in hatching success ($z \geq -4.04$, $p \leq 0.0259$) (Fig. 2.15). There was no effect of year, nearest neighbour distance, or laying order on hatching success. Analysis of only the 2008 data in order to also investigate the effect of nest quality gave the same minimum adequate model, such that nest quality was not a significant determinant of the likelihood of hatching.

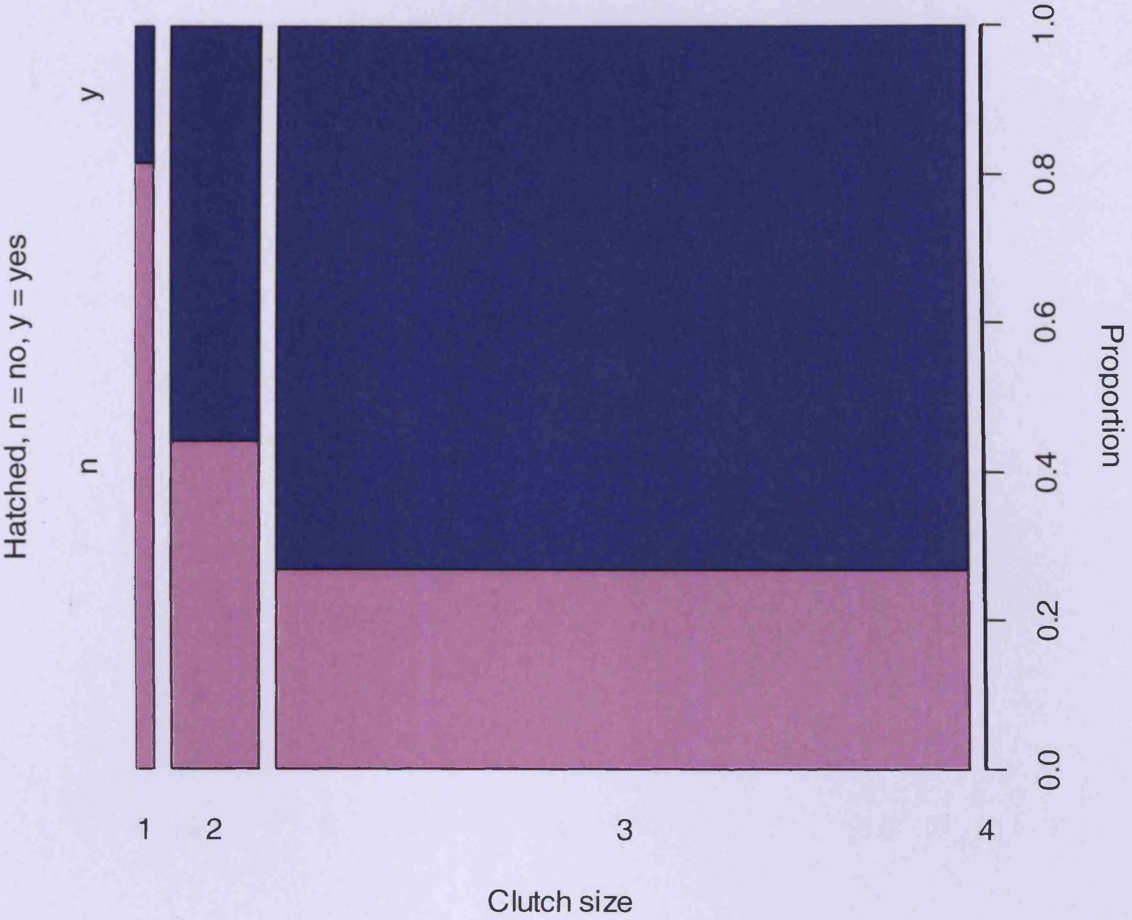

Fig. 2.14. The relationship between hatching success and clutch size. Eggs from larger clutches were significantly more likely to hatch than those from smaller clutches (2007 and 2008 data combined as there was no significant difference between years). Width of columns is proportional to the number of eggs.

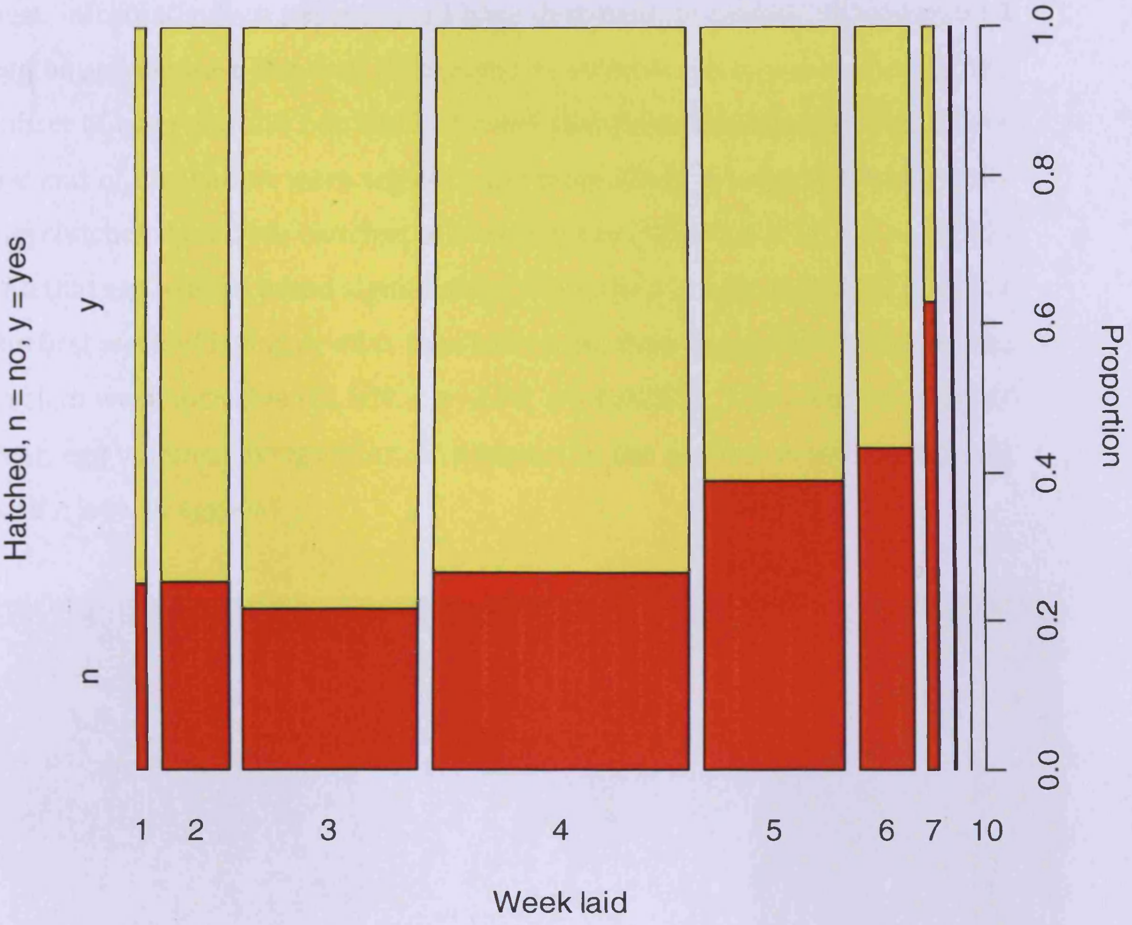

Fig. 2.15. The relationship between hatching success and week of laying. Eggs produced in the early and middle part of the laying season were significantly more likely to hatch than those produced later (2007 and 2008 data combined as there was no significant difference between years). Column width is proportional to the number of eggs.

Hatching failures were typically a result of infertility (i.e. the eggs never hatched), or egg disappearance. The latter affected 11.9% of all eggs recorded in 2007, and 12.1% in 2008 (with 15.6% of eggs infertile in 2007, and 16.0% in 2008). Such disappearances were likely to be partly due to egg theft by other members of the gull colony, which was observed on several occasions (Fig. 2.16). However, egg loss could also have been a result of damage by the parents themselves, brought about by inadequate incubation or sudden movements during disturbances. Certain adults were seen incubating cracked eggs in the days leading up to their disappearance from the nest, indicating that they might have been abandoned or destroyed by their parents. Indeed, some of these eggs were later found pushed out of the nest. Alternatively, a parent could have destroyed or pushed an undamaged egg out of the nest if it was recognized as infertile. A model evaluating the subset of eggs that did not hatch showed that those that disappeared before the end of incubation were significantly more likely to originate from single egg clutches than from clutches of two or three (GLMM, $z = 3.67$, $p = 0.0002$) and that egg loss occurred significantly more often in eggs produced in either the first week of laying or after the sixth week, than in eggs laid in the second to sixth week inclusive (GLMM, $z \geq -2.73$, $p \leq 0.0231$). There was no effect of year, egg volume, laying order, or distance to the nearest neighbouring nest on the level of egg loss.

Fig. 2.16. This Lesser Black-backed Gull has just stolen and eaten an egg (the shell of which is visible on the ground) from a neighbouring nest, in a densely populated region of the Flat Holm gull colony, May 2008.

The gulls in the monitored area appeared to show strong nest site fidelity between one year and the next. Some of these individuals had rings, such that it was possible to confirm that they were indeed the same pair in 2007 and 2008. Others were recognized by their appearance and behaviour. In each year, particular parts of the study area were much more densely populated than other areas (Fig. 2.17). Some of this spatial structure was due to the presence of impenetrable vegetation where nesting was difficult (for instance, the low density patch between approximately 105 m on the abscissa by 20 m on the ordinate in Fig. 2.17 was occupied by thick brambles). Density ranged from 0 to 13 nests per 100 m^2 square of the grid in 2007, and 1 to 14 nests for 100 m^2 in 2008. The most densely populated areas were exposed, open areas, with predominantly rocky or grassy substratum. The overall nest density was 0.0452 m^{-2} in 2007, and 0.0475 m^{-2} in 2008 and differed significantly from CSR in both years ($\chi^2_{76} = 118.43$, $p = 0.0013$ in 2007, $\chi^2_{76} = 143.71$, $p < 0.0001$ in 2008). Mean nearest neighbour distance was 2.59 ± 0.07 m in 2007, ranging from 0.50 m in the mostly densely populated areas, to 8.30 m in the least. The mean for 2008 was also 2.59 ± 0.07 m, with a range of 0.14 m to 7.60 m. There was no significant difference in nearest neighbour distance in the two years (ANOVA, $F_{1,712} = 0.02$, $p = 0.8824$).

Examination of the distribution of nests according to their properties showed that nests with similar characteristics appeared to be placed in the same parts of the colony. Fig. 2.18, for example, shows that the region between approximately 90 m and 100 m on the abscissa, and 0 m to 15 m on the ordinate, had a high density of nests with a clutch size of less than three in both 2007 and 2008. This was a rocky area with little vegetation, and many of the nests here were of a Poor quality. Nests in different parts of the colony also appeared to be locally synchronized with respect to laying date.

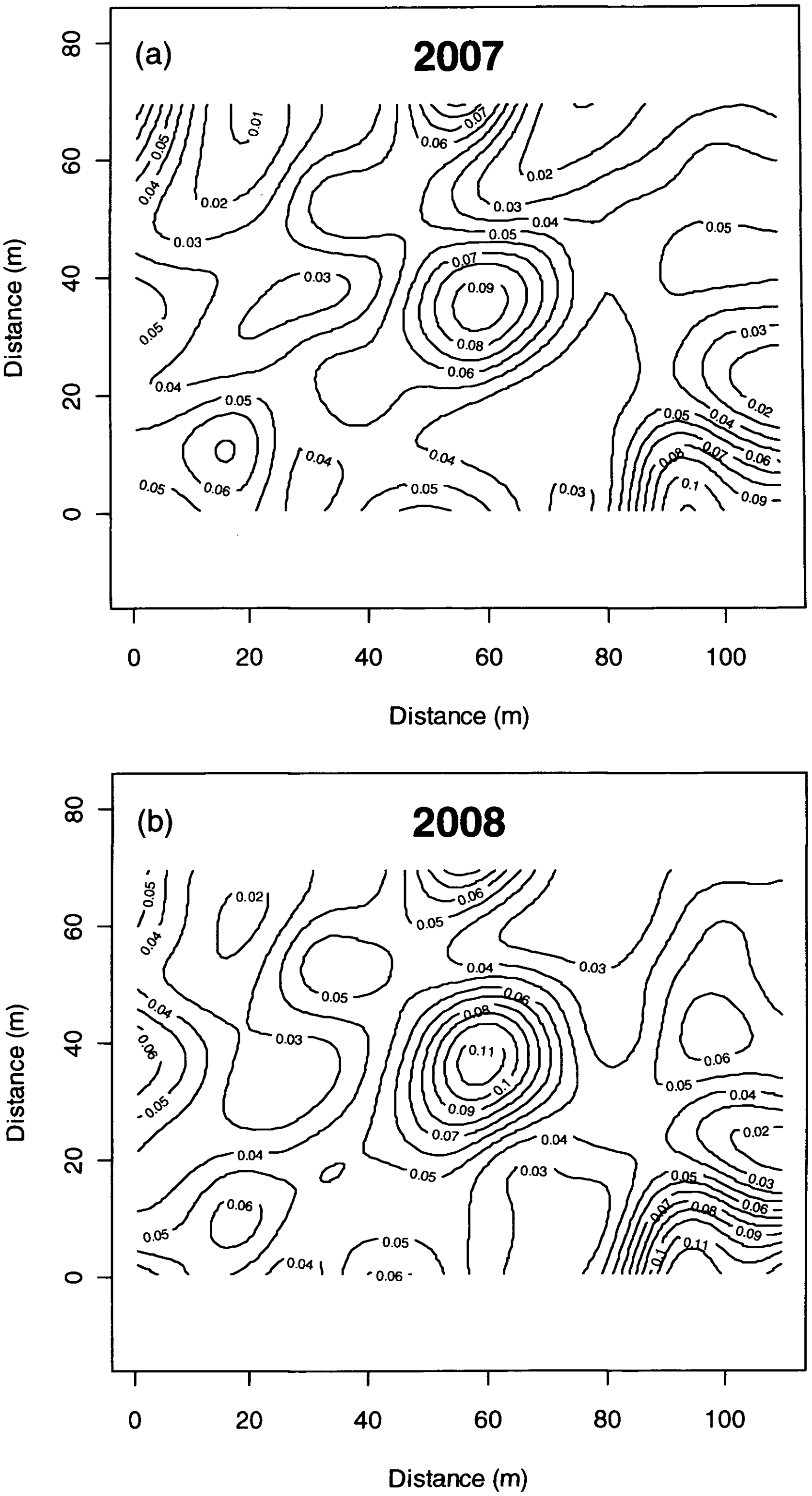

Fig. 2.17. Nest density in the monitored area of the Flat Holm Lesser Black-backed Gull colony in (a) 2007, (b) 2008. Contour lines represent nests m^{-2}. Density was similar in 2007 and 2008, with corresponding areas of high and low nesting activity in each year.

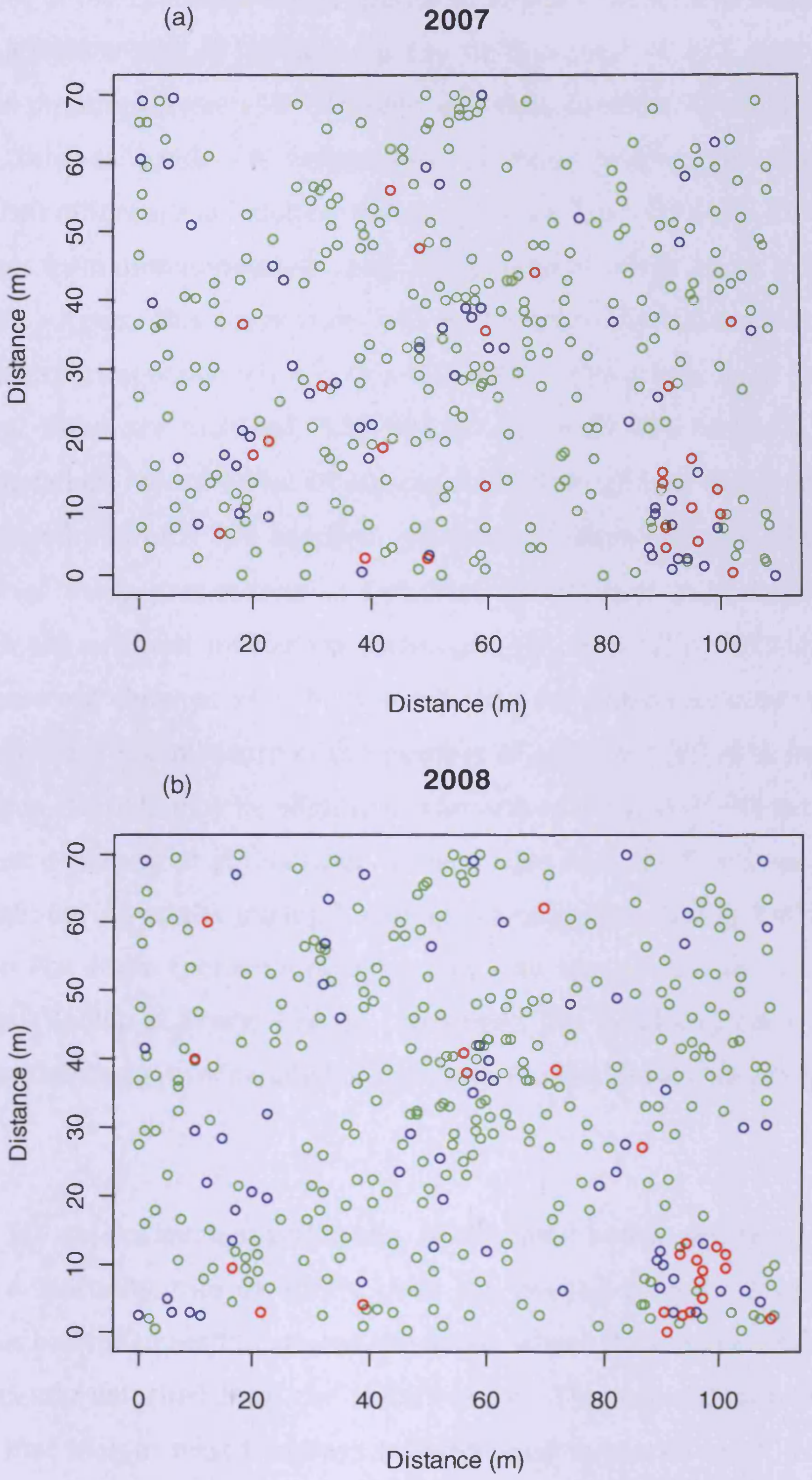

Fig. 2.18. Nest distribution in (a) 2007, (b) 2008 according to clutch size. Green - clutch of 3, blue – clutch of 2, red – clutch of 1.

2.4.2 Chick hatching and rearing

Only four of the 121 pipped eggs subject to artificial incubation did not hatch, giving a failure rate of 3.3%.[14] In the field, a total of 527 eggs attained external pipping between 19th May and 13th June, of which 23 did not hatch, a failure rate of 4.4%. A comparison of these proportions showed no significant difference in hatching failure ($\chi^2_1 = 0.07$, $p = 0.7847$). Considering only eggs from unmanipulated nests, 334 pipped of which 22, or 6.6%, failed to hatch. Again, this proportion was not statistically different from eggs hatched experimentally ($\chi^2_1 = 1.22$, $p = 0.2698$). If only eggs from clutches of two and three are included, 522 pipped of which 501 hatched, giving a hatching failure rate of 4.0%. Of unmanipulated clutches of two or three, 329 eggs pipped of which 309 hatched, a hatching failure of 6.1%. Once again, neither of these proportions is significantly different from eggs hatched through the artificial incubation technique, ($\chi^2_1 = 0.01$, $p = 0.9150$ for all two/three egg clutches, $\chi^2_1 = 0.85$, $p = 0.3554$ for unmanipulated two/three egg clutches). The measure of the number of eggs that failed to hatch after pipping in the field may be slightly conservative, because of the exclusion of eggs that disappeared at this stage, which might have died or been predated by neighbouring adults during hatching (cannibalism during hatching was seen on Flat Holm (personal observation), and has been observed at other colonies (Kadlec & Drury, 1968)). However, the results remain the same whether these eggs are included in the analysis with those that did or did not hatch.

Of the 117 chicks hatched artificially, twelve died before return to the nest, giving a mortality rate of 10.3% over the rearing period. Five of these fatalities had inflammation around the navel, where the amnion and allantois had recently detached from the chick's body. The remaining deaths were chicks that took at least two days to hatch, and appeared weak as soon as they emerged. The equivalent mortality rate in the wild could not be

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[14] In 2007, six pipped eggs from the 91 removed from the colony did not hatch, giving a failure rate of 6.6%. The equivalent figure for the monitored part of the colony could not be ascertained, because of paucity of data.

established, as it was not possible to tell if chicks that disappeared soon after hatching had died due to weakness or predation by neighbours, or were simply too well hidden in the undergrowth. The focus of the work during the chick period was also on behavioural testing, such that less time was available for monitoring activity in the gull colony.

2.5 DISCUSSION

The observations made of nesting behaviour reported in this chapter reveal that the Lesser Black-backed Gulls monitored on Flat Holm formed part of a typical colony of large white-headed gulls in terms of incubation time (MacRoberts & MacRoberts, 1972), egg volume (Harris, 1964; Brown, 1967b; Ryttman *et al.*, 1978) and the proportion of gulls laying clutches of each size (Harris, 1964; Brown, 1967b; Kadlec & Drury, 1968; Verbeek, 1979; Coulson *et al.*, 1982). Clutch size was towards the top end of the range reported (Paynter, 1949; Harris, 1964; Harper, 1971; Gillett *et al.*, 1975; Haycock & Threlfall, 1975; Davis & Dunn, 1976; Pierotti & Annett, 1987), and the proportion of eggs hatching from small clutches was somewhat better than that found elsewhere (Harris, 1964; Haycock & Threlfall, 1975). There was no evidence of any unusual or adverse conditions, such as food shortages, that might have affected breeding behaviour, and although the gulls were subject to a relatively high level of investigator disturbance due to daily visits in the gull colony, hatching success (which was conservatively estimated, as the fate of some eggs could not be ascertained) was comparable to that found in other studies (Paynter, 1949; Harris, 1964; Brown, 1967b; Fordham & Cormack, 1970; Harper, 1971; Haycock & Threlfall, 1975; although Gillett *et al.*, 1975, suggest that investigator disturbance affects chick rather than egg mortality, and only the latter was measured in this study).

2.5.1 Predicting reproductive success from nesting behaviour

The work described here concerned only the initial stages of the breeding process; that is egg production and hatching success. No data were gathered on fledging success or recruitment. Nevertheless, the results do show that certain, often inter-related, observations can predict reproductive success in this early part of the breeding process.

Hatching success, perhaps the most salient measure of reproductive success assessed, was significantly positively associated with egg volume, clutch size and the amount of vegetation cover around the nest. Eggs laid late in the season were also significantly less likely to hatch than those laid earlier.[15] These findings largely echo those from other studies elsewhere, although the reduction in hatching success with decreasing egg size has not always been seen (Nager *et al.*, 2000). Seasonal declines in hatching success have been reported for Kelp Gulls (*L. dominicanus*) (García Borboroglu *et al.*, 2008) and Herring Gulls (Brown, 1967b), as well as for Lesser Black-backed Gulls at British colonies other than Flat Holm (Brown, 1967b; Davis & Dunn, 1976). Similarly, eggs from smaller clutches have been found to be less likely to hatch in Herring Gulls, Western Gulls, Glaucous-winged Gulls, American Herring Gulls and Lesser Black-backed Gulls (Paynter, 1949; Harris, 1964; Brown, 1967b; Harper, 1971; Haycock & Threlfall, 1975; Parsons, 1975a; Sydeman *et al.*, 1991; Murphy *et al.*, 1992). The association seen between hatching success and vegetation quantity was similar to that found in Kelp Gulls by García Borboroglu and Yorio (2004a), and was also in accord with the results of Good (2002), who found that the addition of nest cover improved hatching success in the Western Gull/Glaucous-winged Gull (*L. glaucescens*) hybrid complex. Brown (1967b) observed that eggs next to cover were more likely to hatch than those that were not in Lesser Black-backed Gulls, but did not quantify the amount of cover involved.

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[15] Hatching success was not related to laying order, in agreement with Nager *et al.* (2000) who also worked on British Lesser Black-backed Gulls. However, these authors did find a negative relationship between fledging success and laying order, which was not assessed in the current study.

Analysis of the properties of the non-hatching eggs, showed those eggs that failed to hatch due to disappearance from the nest were more likely to originate from smaller clutches, and to be laid on either side of peak laying. Some of these eggs had previously been found to be broken in the nest. Beer (1961; 1965) noted that gulls with fewer than three eggs rise and resettle more often than those with the modal clutch size, and spend less time sitting on their eggs. These frequent movements might lead to egg damage, while periods of inattentiveness might allow unhealthy fluctuations in egg temperature that reduce the likelihood of hatching success, along with providing opportunities for egg predation. It could be inferred, therefore, that gulls are adapted to incubate the modal clutch size for that species (see also Niizuma *et al.*, 2005), such that any other number of eggs does not provide the correct stimulus to bring about optimal incubation behaviour.

The enhanced egg loss seen both very early and in the last weeks of the laying period, as well as direct observation, suggests that intraspecific predation did play a role in the disappearance of eggs. Such eggs would have been produced before and after peak laying, and thus would not have benefited from the safe-guards against intraspecific predation conferred by synchronised laying (see section 2.1.2). Since it has been found that the pairs that have fallen victim to egg robbery turn to this behaviour themselves in Lesser Black-backed Gulls (Davis & Dunn, 1976), eggs laid late in the season would be especially vulnerable to theft.

As both of the predictors of egg disappearance (clutch size and laying date), improve with age (with older birds producing bigger clutches earlier in the year) (see section 2.1.4) (Davis & Dunn, 1976), the egg loss observed could have been the result of inadequate incubation and brood defence by young, inexperienced parents. Young breeders have been found to suffer high levels of intraspecific nest predation in Yellow-legged Gulls (Oro, 2008). It is also possible that the pairs affected by egg disappearance were of a low phenotypic quality, and were thus unable to lay either large or early clutches, and were similarly incapable of territorial defence under pressure of competition or predation by superior quality birds. Indeed, clutch size has been shown to honestly reflect quality in Western Gulls (Sydeman *et al.*, 1991).

It is interesting that the amount of vegetation around the nest and egg volume both explain overall hatching success, but not the likelihood of egg loss. This suggests that disappearing eggs can be of any size, while those that do not hatch due to infertility or inadequate incubation are more likely to be at the smaller end of the scale. Small eggs are more likely to be laid by young birds (Ryder, 1975; Reid, 1988) that might be more likely to lay infertile eggs, or not yet know how to incubate well enough to ensure hatching.

Correspondingly, eggs that go missing may originate from nests with any range of nearby cover, whereas those that do not hatch are more likely to have little cover. This somewhat counter-intuitive result suggests that egg predation is not the driving force behind egg loss, as increased cover would presumably help to protect the clutch from encroachments by intruders (as suggested by Haycock & Threlfall, 1975; Hunt & Hunt, 1975; Burger & Shisler, 1978). Therefore, the results indicate that egg loss is rather due to other possible causes, for example inappropriate incubation behaviour leading to damage and ultimately rejection by the parents. The main role of vegetation around the nest, therefore, might be to provide and maintain the correct microenvironment for incubation (Kim & Monaghan, 2005), such that eggs with little cover fail to hatch because of unsuitable incubation conditions.

Examination of the second measure of reproductive success, clutch size, revealed a positive trend between this factor and the amount of vegetation surrounding the nest. This is again a finding shared with Good (2002), while a high proportion of nests on bare patches have been found to contain small clutches in Yellow-legged Gulls (*L. michahellis*) (Bosch & Sol, 1998; Oro, 2008). In common with Paynter (1949) and García Borboroglu *et al.* (2008), there was no relationship between the timing of breeding and clutch size, although other studies have reported a decline in this variable over the course of the breeding season (Haycock & Threlfall, 1975; Parsons, 1975b; Kilpi, 1990), including in Lesser Black-backed Gulls (Brown, 1967b; Davis & Dunn, 1976).

The final indicator of reproductive success measured in this study of nesting behaviour was egg volume, which has been shown to relate positively to chick survival (Parsons, 1970; Lundberg & Väisänen, 1979; Bolton, 1991). Egg volume was found to decline over the course of the breeding season, in agreement with studies on Herring Gulls (Parsons, 1972; 1975) and Lesser Black-backed Gulls (Davis & Dunn, 1976). Egg volume was also significantly associated with the appearance of the nest, such that nests with a larger quantity, and more organised arrangement of, nesting material held bigger eggs than nests with a small, scattered and disorganised amount of nesting material. Egg volume was only positively related to clutch size when just the first laid egg was considered, as the differences in egg size with laying order (a significant decline in volume from A to C eggs, in accordance with the findings of Harris, 1964; Parsons, 1970; 1975; Haycock & Threlfall, 1975; Mills, 1979; Schoen & Morris, 1984; Spaans, *et al.*, 1987; Salzer & Larkin, 1990; Kilpi *et al.*, 1996; Nager *et al.*, 2000) clouded the relationship if all eggs were considered.

These results again suggest an association between parental age and egg volume, as younger birds lay smaller eggs and smaller clutches (see section 2.1.4). The relationship between nest appearance and egg size might reflect breeding skills learned with experience too, but also phenotypic quality, as pairs that produced large eggs also had sufficient energy to seek lots of nesting materials and form them into a large, well organised nest.

The non-random spatial distribution found in the nest placement of the Lesser Black-backed Gulls monitored is typical for seabird colonies (Patterson, 1965; Harper, 1971; Pierotti, 1982; Bosch & Sol, 1998; Kokko *et al.*, 2004; Oro, 2008). However, the density of nests in this study was high compared to that reported for other large white-headed gulls, both in terms of the mean and peak densities found (Haycock & Thelfall, 1975; Murphy *et al.*, 1992; Jehl, 1994). In both years, the most densely populated regions were open, grassy or rocky areas, with no tall vegetation. It appears that there was some assortative clustering in the colony, such that birds distributed according to their quality. In both 2007 and 2008, there seemed to be an aggregation of birds laying less than the modal clutch size of three eggs (approximately one quarter of pairs in each year) in a bare rocky area in the north-west corner of the area surveyed. Observation of the birds breeding in this area revealed that some had vestiges of sub-adult plumage (see Malling Olsen and Larsson (2004) for details of aging Lesser Black-backed Gulls from their appearance), indicating that they may have been recent recruits to the colony (Fig. 2.19). This is consistent with the results of a study in Yellow-legged Gulls, which showed that young birds were more likely to nest in open, non-vegetated areas (Oro, 2008), while the height of vegetation around the nest has been found to co-vary with age in Glaucous-winged Gulls (Reid, 1988).

It is therefore possible that birds in the colony were clustering according to their age. This in turn might be because young breeders were unable to exploit nesting habitats in other parts of the colony, as they were out-competed in territorial establishment by older birds. Nests in the monitored area might therefore have been spaced according to an ideal despotic distribution (Fretwell & Lucas, 1970), in common with recent findings in the closely related Yellow-legged Gull (Oro, 2008). The particular areas where birds with a small clutch size congregated were also densely populated, indicating that if birds were recruiting to these patches, they might have been drawn by attraction to breeding conspecifics (Brown, 1967a; Chabrzyk & Coulson, 1976; Oro & Pradel, 2000; Greene & Stamps, 2001; Oro, 2008). Territory size has been shown to increase with age in Glaucous-winged Gulls (Reid, 1988), although the opposite effect was found for Herring Gulls, with individuals recruiting to low density patches and then moving to preferred higher density areas when they became more established (Chabrzyk & Coulson, 1976).

Fig. 2.19. One of the individuals breeding in the densely populated bare, rocky area of the monitored area, in which pairs producing a small clutch size appeared to congregate. Clear signs of sub-adult plumage can be seen on the wings, indicating that this bird is a recruit.

There were no effects of nearest neighbour distance, which was used as a proxy for nest density, on any of the parameters measured in this study. This finding is consistent with the lack of density dependence on the breeding success of gulls in a number of other studies (Patterson, 1965; Dexheimer & Southern, 1974; Hunt & Hunt, 1975; Jehl, 1994). However, as discussed in section 2.1.3, a complex relationship has been found between nest density and reproductive success, the nature of which depends on many factors that were beyond the remit of this work.

The breeding parameters measured on Flat Holm indicated a healthy colony, such that the gulls laid large clutches containing sizeable eggs despite living at a high density (a negative relationship between egg volume and density has previously been described (Coulson *et al.*, 1982; Spaans *et al.*, 1987)). These factors were also highly consistent between years, suggesting stable environmental conditions. Furthermore, the level of egg loss found was lower than that seen at colonies with a similar density, and was instead equivalent to that of lower density colonies (e.g. Haycock & Threlfall, 1975), perhaps indicating that the gulls in this study were not impelled through food shortage to eat each others' eggs. Not only do the gulls on Flat Holm have protected status, they have access to plentiful and predictable food supplies throughout the Severn Estuary and Bristol Channel region. The edible waste generated by the cities of Cardiff, Newport and Bristol, and surrounding towns, is within flying distance of Flat Holm, such that the island's gulls should not have difficulty consuming the food required for successful egg production. It appears, therefore, that all but the lowest quality and youngest breeders are capable of successful breeding until the hatching stage.

2.5.2 Chick hatching and rearing

The results show that it is possible to take pipped gull eggs from the wild and hatch them successfully, with only simple equipment and limited control over environmental conditions. The hatching failure rate of pipped eggs was not significantly different using the experimental technique when compared to either (a) all eggs in the field, (b) those in unmanipulated nests only, or (c) eggs from clutches of two or three (in both manipulated and unmanipulated nests). Although the level of chick mortality in the wild over the period equivalent to the experimental rearing time (approximately two days) could not be assessed, the mortality rate of 10.3% observed during experimental rearing compares favourably to that found by Bolton (1991), who documented a mortality rate of approximately 10% two to three days post-hatching for Lesser Black-backed Gull chicks in cross-fostered clutches (surrounded by wire fences) at the Flat Holm colony. Records from Lesser Black-backed Gulls at British colonies elsewhere, where nests were monitored but eggs not manipulated, show a substantial mortality rate in early life, affecting 37% of chicks during the first week (Davis & Dunn, 1976) and 44% during the first ten days post-hatching (Brown, 1967b), while Griffiths (1992), who enclosed nests and took blood samples post-hatching, found a 24.3% mortality rate after three days. Similar figures have been reported for the Herring Gull in the UK and American Herring Gull in the USA and Canada (Brown, 1967b; Kadlec & Drury, 1968; Davis, 1975a; Haycock & Threlfall, 1975).

Since the experimental method for hatching and rearing chicks was effective, it could be useful to fieldworkers in remote areas studying other species, especially those with precocial and semi-precocial young, where rearing is less demanding than in altricial species (O'Connor, 1984). The technique could be particularly beneficial to researchers wishing to keep chicks naïve to factors that they would normally experience during development. In this case, the object of the study was to examine innate behaviour. However, the method could be adapted for studies of other aspects of chick biology, such as the effect of diet, hormones or environmental contaminants on chick growth and development.

Chapter 3

Experimental investigation of the role of adult bill colouration in the chick pecking response in Lesser Black-backed Gulls (*Larus fuscus*)

3.1 INTRODUCTION

The chick pecking response is a type of innate behaviour seen in the young of several different species of precocial and semi-precocial birds (O'Connor, 1984). These species can pick up and manipulate food themselves from hatching, and hence exhibit active preferences for particular food items consumed, unlike altricial chicks which are incapable of handling food independently (O'Connor, 1984; Starck & Ricklefs, 1998). The pecking response has been studied in several species, including quail (*Coturnix* spp.), domestic chickens (*Gallus gallus domesticus*) (Bolhuis, 1991; Gamberale-Stille & Tullberg, 2001; Ham & Osorio, 2007), and members of the Family Anatidae (namely ducks and geese) (Kear, 1964). However, some of the seminal work in this field has been carried out with larids, notably the Herring Gull (*Larus argentatus*), which was the model species in the pioneering studies of Niko Tinbergen and co-workers in the mid-twentieth century (Tinbergen & Perdeck, 1950; Tinbergen, 1953). In its simplest form, the larid pecking response occurs when a chick pecks at its parent's bill to bring about the delivery of food. This may either be through regurgitation of previously ingested foodstuffs, as is the case in gulls and some tern species (Tinbergen & Perdeck, 1950; Cullen, 1962; Hailman, 1967), or the provision of fresh food, seen in other terns (Quine & Cullen, 1964). If the adult in question comes from a species with prominent bill markings, such as spots, stripes or differently coloured tips, the chick typically orientates its pecking response towards these features (Tinbergen & Perdeck, 1950; Hailman, 1967).

3.1.1 Begging and parental care in birds

The pecking response is one of a number of behavioural patterns observed in newly hatched chicks of various species, as a means of obtaining food from their parents. Such behaviour is commonly referred to as begging. The type of begging observed and the extent to which it is performed depends partly on the degree of development of the chicks of the species concerned at hatching (O'Connor, 1984).

The progeny of many animals, including reptiles, mammals and birds, can be classified according to the level of independence from their parents that they exhibit at the beginning of life. Young that are immediately able to fend for themselves are termed precocial, while feeble, vulnerable young requiring extensive parental care are known as altricial, although the exact categorization of species on this spectrum is subject to debate (Starck & Ricklefs, 1998).

In birds, precociality is thought to be the ancestral state (Temrin & Tullberg, 1995). It is found in several orders, including the Galliformes, Charadriiformes, Anseriformes and Struthioniformes (O'Connor, 1984). The most impressive case of precociality is perhaps that seen in species of the Family Megapodiidae, such as the Australian brush-turkey (*Alectura lathami*), whose eggs are not incubated by their parents, but by geothermal heat or that produced by microbial decomposition of organic matter (Göth & Evans, 2005). Chicks receive no parental care at all once hatched, and are therefore at an advanced stage of development. They have good vision, feathers ready for flight, are capable of thermoregulation, and have the innate ability to locate and consume food. Such species are sometimes referred to as superprecocial (for a discussion, see Göth, 2002). Less extreme forms of precociality are seen in families such as the Anatidae and Charadriidae, where chicks have a good covering of down, the ability to walk, swim and find food, but imprint on and follow one or both of their parents, who they depend on for brooding and protection (Bolhuis, 1991; O'Connor, 1984; Starck & Ricklefs, 1998). The young of families such as the Phasianidae and

Meleagrididae are slightly less independent again, requiring their parents to indicate the presence of food, while adults of families including the Rallidae and Podicipedidae offer food to their chicks (Starck & Ricklefs, 1998). As the offspring of precocial species depart from the nest immediately following hatching, they are referred to as nidifugous (O'Connor, 1984).

At the other end of the spectrum lie species with altricial chicks, which include all Passeriformes, Psittaciformes and Coraciiformes (O'Connor, 1984). Such chicks often hatch naked, with their eyes closed and apart from begging, exhibit little motor activity (Starck & Ricklefs, 1998). Since altricial young are unable to leave the nest, they are termed nidicolous (O'Connor, 1984). A greater degree of parental care is required by altricial chicks, since they are wholly dependent on adults for feeding, protection and thermoregulation (O'Connor, 1984). Such dependence may in part explain why cooperative breeding, where more than two adults care for chicks, is relatively common in species with altricial young (Cockburn, 2006), while short-term pair bonds are more frequent in precocial species (Temrin & Tullberg, 1995).

Gull and tern chicks are semi-precocial,[16] that is their eyes are open at hatching, they have a downy covering for basic thermoregulation, and they are able to walk (but not swim or fly). They do not, however, follow their parents away from the nest after hatching as do fully precocial young, but instead remain in or near their parents' breeding territory until fledging,[17] and are therefore termed semi-nidifugous (Cramp & Simmons, 1983). They are also entirely dependent on their parents for the provision of food (Tinbergen, 1953; Spaans, 1971; Bukaciński *et al.*, 1998; Starck & Ricklefs, 1998), and do not feed wholly independently until several weeks post-fledging (Burger, 1981; Spear *et al.*, 1986). Parental care is provided by both

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[16] Larid chicks are occasionally referred to as semi-altricial, after Skutch (1976) (cited in Starck & Ricklefs, 1998).

[17] Sabine's Gull (*Xema sabini*) is an exception to this rule, with parents leading their chicks away from the nest a few days after hatching (Brown *et al.*, 1967).

the male and the female, as neither parent alone can successfully raise young (Furness & Monaghan, 1987). Each parent in turn departs on foraging trips[18] (Spaans, 1971; Morris, 1987; Bukacińska *et al.*, 1996), returning with the food that they then regurgitate for their young when the latter beg (Tinbergen & Perdeck, 1950). Unsolicited chick feeding is sometimes seen too (Brown *et al.*, 1967; Hario & Rudbäck, 1999). Larid hatchlings are also reliant on their parents for defence against predators (although chicks may move away from the nest and hide) (Tinbergen, 1953), and maintaining their body temperature when faced with fluctuating weather conditions (Impekoven, 1969; Beer, 1970a; Dunn, 1976; Lee *et al.*, 1993; Visser, 1998).

In species where the young exhibit any degree of dependence on their parents for feeding, there must be selection for the evolution of an effective signalling mechanism between parents and offspring to ensure that the young are sufficiently nourished for growth and development (Godfray, 1995; Kölliker *et al.*, 2005). Begging represents the chick's role in such a system, while the parents may have various coadaptations for addressing their progeny's needs, depending on the species concerned (Kölliker & Richner, 2001; Kölliker *et al.*, 2005).

The form, strength and elaborateness of this communication between parents and their offspring depends on many factors, including brood size (Krebs & Putland, 2004; Mathevon & Charrier, 2004), kin relatedness (Briskie *et al.*, 1994), the presence of brood hierarchies (O'Connor, 1984), how much of a parent's reproductive effort is concentrated in a specific breeding event (i.e. the likely effect of chick survival on a parent's lifetime reproductive success (Lessells, 1991)) and the degree of precociality seen in the offspring (O'Connor, 1984). There has been much discussion in the literature over the nature of begging in altricial birds in particular, with focus on the evolution and costs of this behaviour, and whether it honestly reflects a chick's needs to its parents (Godfray, 1991; Kilner *et al.*, 1999; Godfray & Johnstone, 2000).

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[18] Once chicks reach about three weeks old, parents forage simultaneously (Emlen, 1956; Spaans, 1971).

Less research has been carried out into the parental role in this communication, or how the system operates in precocial species (but see Lyon *et al.*, 1994; Krebs & Putland, 2004).

In gulls, the communication between chicks and their parents over food is a two-way process, with both parties signalling to each other using various sensory modalities. Similar behavioural patterns are seen in species of tern (Cullen, 1962; Quine & Cullen, 1964). The chick's primary role in the interaction is that of repeated pecking at the parent's bill, providing tactile and visual stimuli to bring about regurgitation of food, which is then either taken from the ground, or from the parent's beak (Tinbergen & Perdeck, 1950; Tinbergen, 1953).[19] The chick's pecks are accompanied by persistent, high-pitched "peeping" vocalizations, and frequently small flapping movements of the wings and/or a rapid up and down movement of the head[20] (Tinbergen, 1953; Henderson, 1975; Groothuis, 1989a). The parent, meanwhile, may initiate the pecking response through the production of a drawn-out, falling vocalization known as the "mew" call, which is always produced during chick feeding, and the adoption of a characteristic feeding posture, with the body crouched and the neck stretched towards the ground (Tinbergen, 1953; Evans, 1970; Henderson, 1975).

In approximately 62% of gull species, breeding adults have some form of distinctive bill colouration (Fig. 3.1) (Ferns & Ross-Smith, 2009). This commonly takes the form of either stripes or tips that are of a different colour from the rest of the bill, or a prominent patch of red on an otherwise yellow lower (and sometimes upper) mandible known as the gonys spot. The latter is only found in a monophyletic subset of species that make up the large

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[19] In some species, for instance the Black-legged Kittiwake (*Rissa tridactyla*) chicks take regurgitated food from the parent's throat as an adaptation to cliff nesting, as chicks risk falling from the nest if they move around too much (Cullen, 1957; Cullen & Cullen, 1962).

[20] This head "pumping" or "bobbing" is seen more often as chicks grow older (Henderson, 1975; Groothuis, 1989a).

white-headed gulls (Fig. 1.1).[21] These bright, contrasting bill colours act as a visual signal, providing a focus for chick pecking (Tinbergen & Perdeck, 1950; Brown *et al.*, 1967), and reinforcing the vocalizations and movements which parents make in communicating with their chicks over feeding.

Fig. 3.1. Adult bill colouration during the breeding season in five species of gull. Left to right: Ring-billed Gull (*Larus delawarensis*), Swallow-tailed Gull (*Creagrus furcatus*), Herring Gull, (*Larus argentatus*), Laughing Gull (*Leucophaeus atricilla*), Ivory Gull (*Pagophila eburnea*). Photographs downloaded from www.oiseaux.net (Ring-billed Gull - © Luc Durocher, Herring Gull - © Jean-Michel Fenerole, Laughing Gull - © Manuel Presti).

In common with many animal signals therefore, parent-offspring communication in gulls involves a combination of physical attributes and production of simple, repetitive, ritualised and redundant movements and sounds to render the message conveyed as detectable and discriminable (Krebs & Dawkins, 1984; Zahavi, 1987; Guilford & Dawkins, 1991). The bright bill markings seen in adults of certain species may serve to amplify the effect of the parental signal (Zahavi, 1987). Such "multimodal" signalling (Partan & Marler, 1999) can also increase the efficiency of the message transmission, as interactions between the signal's components in each sensory modality may potentiate information transfer in comparison to the summed effect the same components presented in isolation (Guilford & Dawkins, 1991; Guilford & Dawkins, 1993; Partan & Marler, 1999). Importantly, the appearance of the parental bill taps into a powerful innate response in the chicks, such that no learning is required to perform pecking behaviour (Tinbergen & Perdeck, 1950; Hailman, 1967; Krebs & Dawkins, 1984; Guilford & Dawkins, 1991).

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[21] Approximately 20 species make up the large white-headed gulls, although the exact number is uncertain because of frequent reclassifications (section 1.4).

3.1.2 Factors influencing the pecking response

Several studies have shown that the phenotype of young chicks, including aspects of their begging behaviour, can be both modified post-hatching and affected by extrinsic factors determined before a chick has even hatched.

3.1.2.1 PREDETERMINED FACTORS AND PECKING BEHAVIOUR

Chick begging phenotype is likely to be influenced in part by its parents. This can be due to genetic inheritance, in that high quality parents might be likely to produce robust offspring, which are able to beg enthusiastically. Offspring phenotype could also be affected by that of its parents during a given breeding attempt. There is mounting evidence that parental phenotype is transmitted to offspring through maternally-mediated adjustments in egg production (Gasparini *et al.*, 2001; 2007; Groothuis *et al.*, 2005), which both reflect the capabilities of parents to rear chicks (Nager, 1999), and which best equips chicks for life under the prevailing external conditions, both inside and outside the nest (Eising & Groothuis, 2003; Müller, 2004a). Thus, correlates of parental quality and phenotype could translate to differences in the chick pecking response.

The influence the egg has on offspring phenotype has received particular attention in the literature. Like other larids, gulls normally lay three eggs[22] per breeding season (Tinbergen, 1953; Parsons, 1970; Hunt & Hunt, 1973a), although a minority of species, including Black-legged Kittiwakes (Cullen, 1957), Black-billed Gulls (*Chroicocephalus bulleri*) (Beer, 1965), Black-tailed Gulls (*L. crassirostris*) (Niizuma *et al.*, 2005), and Lava Gulls (*L. fuliginosus*) (Snow & Snow, 1969) have a modal clutch size of two, while Swallow-tailed Gulls lay only a single egg per breeding attempt (Snow & Snow, 1967; Harris, 1970). In those species with a modal clutch size of three, eggs are usually laid every other day (Muck & Nager, 2006), but hatch more synchronously, as

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[22] Clutches greater than three are sometimes found, but these are usually the result of female-female pairings, polygyny, or intraspecific nest parasitism rather than egg production by a single male-female pair (Hunt & Hunt, 1977; Shugart, 1980; Betleja *et al.*, 2007; Duda *et al.*, 2008).

parents do not incubate their clutch full-time until all eggs are laid (Beer, 1962), and chicks from the third laid egg (termed the C egg) have an accelerated rate of development relative to the first and second laid (A and B) eggs (Muck & Nager, 2006). Chicks from the A and B eggs thus emerge within hours of each other, while the C chick often hatches one to two days later (Hahn, 1981; Pierotti & Bellrose, 1986; Muck & Nager, 2006).

The laying and hatching asynchrony, along with other within clutch differences between eggs, can give rise to brood hierarchies, where larger, older chicks have a competitive advantage over their siblings in obtaining food from their parents (Muck & Nager, 2006). This had led to speculation that gulls operate a brood reduction strategy (O'Connor, 1984; Stenning, 1996), whereby under good environmental conditions with plentiful food available all chicks can survive, but otherwise small chicks act as insurance of parental reproductive success in case of death of a sibling (Graves *et al.*, 1984), or die quickly if such insurance in not required, so that parental effort can be concentrated on the larger, fitter members of the brood in which they have made most investment (Hahn, 1981; Royle & Hamer, 1998; Royle *et al.*, 2001). However, studies have shown that within-clutch differences are adaptive for maximizing the survival of each chick during a breeding attempt (Reid, 1987; Hillström *et al.*, 2000), and no evidence of parental discrimination between chicks during feedings has been found (Davis & Quinn, 1997; Hario & Rudbäck, 1999), which could be expected if brood reduction was in progress. High quality pairs, or the general population under favourable conditions, can effectively eliminate brood hierarchies altogether, suggesting that gulls lay three eggs simply to maximize their reproductive success rather than as insurance (Pierotti & Bellrose, 1986; Sydeman & Emslie, 1992).

Offspring production is energetically costly (Monaghan & Nager, 1997). As gulls are monogamous, this cost is borne by both members of the pair, who share in egg incubation duties and chick rearing (Beer, 1961; 1962; 1965; Burger, 1974; Pierotti, 1981; Niebuhr & McFarland, 1983; Morris, 1987;

Bukacińska *et al.*, 1996). Female physical condition is important, as her protein and nutrient reserves are mobilized during egg production, thus limiting egg size, number and viability (Houston *et al.*, 1983; Monaghan *et al.*, 1995; Blount *et al.*, 2004). Indeed, the quality of eggs laid can be enhanced experimentally through supplementary feeding (Bolton *et al.*, 1992; Van Klinken, 1992; Blount *et al.*, 2002; Verboven *et al.*, 2003). Males assist their partner in attaining the physical condition required for egg production through courtship feeding (Tasker & Mills, 1981; Salzer & Larkin, 1990; Mills, 1994; Kilpi & Byholm, 1995), which also imposes costs through depletion of lipid reserves (Hario *et al.*, 1991). Evidence of the demands of offspring production in both sexes can also be seen in the fall in body condition during the reproductive period (Monaghan *et al.*, 1998; Moe *et al.*, 2002), as well as in the increased rates of mortality following breeding (Pugesek, 1983; Golet *et al.*, 1998), and the reduction in reproductive success brought about through experimentally increased egg production (Monaghan *et al.*, 1998).

Constraints on egg production have implications for chick survival. This is normally manifested in within-clutch differences in survivorship. Egg size predicts chick condition and survival in early life (Parson, 1970; Pierotti, 1982; Bolton, 1991; Bolton *et al.*, 1992), and the C egg is usually significantly smaller than the A and B eggs (e.g. Parsons, 1970; Mills, 1979; Kilpi *et al.*, 1996), giving rise to significantly lighter and skeletally smaller chicks at hatching (Hébert & Barclay, 1988; Davis & Quinn, 1997; Nager *et al.*, 2000; Ležalová *et al.*, 2005). C eggs have lower yolk lipid levels and different lipid fractions from A and B eggs, with a significant reduction in cholesterol (Royle *et al.*, 1999; Nager *et al.*, 2000). The yolk of C eggs also contains significantly smaller amounts of both carotenoids and vitamin E, which act as antioxidants (Royle *et al.*, 1999), and immunoglobulins, which impart passive immunity from mother to chick (Müller *et al.*, 2004). However, C eggs have significantly higher levels of testosterone and other androgens than A or B eggs (Royle *et al.*, 2001; Groothuis & Schwabl, 2002).

Some of the knock-on effects of these intra-clutch differences in egg composition can be seen in chick begging behaviour. The evidence concerning the direction of these effects is mixed. Perhaps the most clear-cut results suggest that begging is adversely affected in C chicks. Their rate of pecking soon after hatching is lower than that of A and B chicks in Yellow-legged Gulls (*L. michahellis*), with a diminished pecking rate also seen in chicks from small eggs, the size typical of Cs (Alquati *et al.*, 2007). C chicks are also less able to manipulate food than A and B chicks (Hillström *et al.*, 2000). Furthermore, there could be more subtle detrimental effects on chick begging associated with coming bottom in the brood hierarchy. The reduced concentrations of antioxidants and immunoglobulins in C eggs could leave chicks vulnerable to physiological stress, bringing about secretion of corticosterone, the avian stress hormone (Landys *et al.*, 2006). Injection with corticosterone has been shown to reduce the intensity of chick begging displays in gulls (Rubolini *et al.*, 2005; but see Kitaysky *et al.*, 2001). Increased likelihood of death in early life (Parsons, 1970; Hario & Rudbäck, 1999) could also decrease C chicks' ability to beg if they become feeble prior to death. Indeed, chicks from last laid eggs have been found to be in a poorer condition than chicks from earlier laid eggs regardless of egg size in Lesser Black-backed Gulls (Nager *et al.*, 2000).

Conversely, an experimental increase in yolk androgens, encompassing levels found in C eggs, has been found to enhance begging behaviour (Eising *et al.*, 2003; Boncoraglio *et al.*, 2006). This could be adaptive for C chicks when competing for food with their older siblings (Eising *et al.*, 2001). Herring Gull C chicks have been seen to behave aggressively towards their siblings in food contests under relatively benign environmental conditions with a low degree of hatching asynchrony (Davis & Quinn, 1997), while they were found to solicit food as often as their older siblings in a different study, although they neglected their parents' regurgitates more frequently than did the older chicks (Hario & Rudbäck, 1999). C chicks also have larger dorsal neck muscles than A and B chicks (Muck & Nager, 2006), which could improve their pecking ability.

Androgens, particularly testosterone, can also act as immunosuppressants (Ros *et al.*, 1997; Groothuis *et al.*, 2005; Müller *et al.*, 2005b), which in combination with C chicks' susceptibility to oxidative stress and reduced maternal antibody inheritance, could increase their vulnerability to pathogens (Royle *et al.*, 2001; Müller *et al.*, 2005a). Indeed, C chicks suffer significantly higher prefledging mortality than do A or B chicks (Parsons, 1970; Parsons, 1975a; Hébert & Barclay, 1988; Nager *et al.*, 2000). Such chicks may not be able to exhibit strong pecking responses. However, no association was found between pecking rate and antioxidant capacity in two-day old Yellow-legged Gulls (Rubolini *et al.*, 2006).

The potential phenotypic effects of egg compositional differences on begging could also be influenced, and compounded, by a chick's sex (Bogdanova & Nager, 2008). Males have higher testosterone levels and show a more marked decline in yolk antibodies with hatching order than females (Müller *et al.*, 2004). Males are also more prone to prefledging mortality than females (Sayce & Hunt, 1987; Müller *et al.*, 2005c), with a substantial proportion of these deaths occurring at the nestling stage (Griffiths, 1992), when the pecking response is seen. Of those C chicks that survive, males fledge in poorer condition than females (Bogdanova & Nager, 2008).

Differences in egg composition also relate to parental nesting behaviour. Eggs produced by pairs on the periphery of a colony, and those with high vegetation cover around their nests, have elevated yolk androgen levels (Groothuis & Schwabl, 2002), while yolk antibody concentrations have also been found to correlate with breeding density (Müller *et al.*, 2004). Furthermore, the social environment of breeding females affects both egg mass and yolk carotenoid levels, which vary with the number of intraspecific interactions in which a breeding female is involved (Verboven *et al.*, 2005). Both nest sites towards the periphery of the colony and those in very densely populated areas tend to be suboptimal, as they are more prone to disturbance and predation (Montevecchi, 1978; Butler & Trivelpiece, 1981; Kazama, 2007).[23] Such sites are therefore usually occupied by low quality pairs (Coulson, 1968; Montevecchi, 1978), which also tend to occupy more exposed nests without good access to adequate take-off and landing areas (García Borboroglu & Yorio, 2004b; Kim & Monaghan, 2005). Low quality pairs may produce more feeble chicks, which do not exhibit a strong pecking response.

3.1.2.2 POST-HATCHING MODIFICATION OF PECKING BEHAVIOUR

Newly hatched chicks in several species exhibit innate preferences for particular forms and colours (Tinbergen & Perdeck, 1950; Kear, 1964; Bolhuis, 1991). In larids, certain properties known as "releasers" have been shown to initiate the pecking response. These manifest as an attraction to long, slender, vertically orientated, striped or spotted and often red objects, that are moved at eye level (Tinbergen & Perdeck, 1950; Cullen, 1962; Conover & Miller, 1981; Margolis *et al.*, 1987). Whether or not this behaviour is adaptive is addressed in Chapters 4 and 5. It is clear, however, that chicks' innate preferences, both in gulls and other precocial and semi-precocial species, are subject to rapid modification upon behavioural stimulation (Evans, 1979; Alessandro *et al.*, 1989; Bolhuis, 1991).

One of the simplest and fastest ways in which such modification takes place is via habituation. This is a form of nonassociative learning, which occurs when an animal is exposed once or repeatedly to a single type of benign stimulus, such that the behavioural response induced decreases in magnitude (Kandel *et al.*, 2000). This has been observed in studies of the pecking response, where chicks' responses to various models have diminished over the course of the experiment (Nyström, 1973; Margolis *et al.*, 1987; Alessandro *et al.*, 1989; ten Cate *et al.*, 2009). Tinbergen and Perdeck (1950) also noted this phenomenon, and referred to it as "negative conditioning".

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[23] Offspring body condition and immunocompetence are negatively associated with nesting density in colonially nesting Magellanic Penguins (*Spheniscus magellanicus*) (Tella *et al.*, 2001).

Chick pecking behaviour is also subject to associative learning, whereby animals develop a response upon the temporal pairing of two stimuli (Kandel *et al.*, 2000). In the case of the pecking response, these two stimuli are food (the unconditioned or sign stimulus, towards which the chick innately directs pecks, in a behaviour known as the unconditioned response or motor programme) and a particular model (the conditioned stimulus, towards which a chick learns to direct its pecks after the reinforcement with food, called the conditioned response) (Margolis *et al.*, 1987). As this form of associative learning occurs after a food reward, it is termed appetitive classical conditioning (Kandel *et al.*, 2000). Such conditioning can override chicks' innate preferences, causing them to peck most strongly towards a stimulus that they do not initially find as attractive as other stimuli after several days of food reinforcement (Weidmann, personal communication, cited in Hailman, 1967). However, for this to occur, such a stimulus must attain a certain threshold in its capacity to release pecking behaviour in naïve hatchlings, even if the initial response observed is not very pronounced (Margolis *et al.*, 1987). Through conditioning, both American Herring Gull and Laughing Gull chicks have been trained to peck preferentially at models of heterospecific adult heads (Hailman, 1967; Margolis *et al.*, 1987; Alessandro *et al.*, 1989), while the pecking preferences of a Black-headed Gull (*C. ridibundus*) chick reared by Black-legged Kittiwake parents have been shown to fall into line with those of Kittiwake chicks by three days post-hatching (Cullen & Cullen, 1962). Chick vocal and approach behaviour has also been found to be strongly influenced by conditioning in the American Herring Gull (Evans, 1979; 1980).

Another form of associative learning that may occur in the pecking response is conditioned inhibition, which results when an animal learns that a particular stimulus predicts the absence of positive reinforcement through, for example, food (Margolis *et al.*, 1987). Thus, hatchling Black-headed Gulls peck at their parent's red bill to initiate feeding, as the bill is a strong releaser for pecking. However, if there is no food reward, this stimulus loses its releasing power (Weidmann, 1959, cited in Beer, 1969a). Similarly, five to six day old Laughing Gull chicks which are exposed regularly to unreinforced models of adult heads show a marked decline in their pecking response to this model compared to chicks of the same age which are naïve to this model. It is difficult to discern the potential roles of habituation and conditioned inhibition in this observation, however (Margolis *et al.*, 1987).

Conditioning is potentiated through multimodal stimulation. Thus, chicks learn positive associations between a particular head model and food more effectively if a recording of an adult call is also played (Griswold *et al.*, 1995). Such conditioning might account for some of the examples in the literature of wild-reared chicks responding differently from naïve hand-reared chicks when presented with the same stimulus (Hailman, 1967; Conover & Miller, 1981), although parental recognition and neophobia play an ever more important role with age as chicks of many species learn to identify their parents through both visual and auditory cues at less than a week old (Beer, 1969b; 1970a; 1970b; Evans, 1970; Conover & Miller, 1981; Evans, 1986; Knudsen & Evans, 1986; Griswold *et al.*, 1995; Charrier *et al.*, 2001; Mathevon *et al.*, 2003). Chicks also begin to recognize their nest sites as early as two days post-hatching (Noseworthy & Lien, 1976; Conover & Miller, 1981), meaning that unfamiliar environmental cues might affect wild-reared chicks' pecking behaviour if individuals are subject to experiments away from the parental nest.

Filial imprinting is a form of learning that is sometimes described as associative (for a review, see Bolhuis, 1991). It is found in several precocial bird species, and occurs when the social behaviour of a chick is limited to a particular object, or class of objects (usually a chick's parent), after unreinforced exposure to that object at a particular point in early life known as the sensitive period (Bolhuis, 1991). There is, however, no evidence that this form of learning takes place in gull chicks (Margolis *et al.*, 1987; Alessandro *et al.*, 1989).

Although the pecking response, along with other aspects of begging behaviour, is subject to learning, spontaneous changes are also seen as chicks mature, which are mediated by ontogenetic processes (Tinbergen, 1953; Moynihan, 1959; Hailman, 1967; Groothuis, 1989a; 1989b). This may occur even in the absence of prior exposure to stimuli. Thus, improvement of motor coordination to a maximum asymptote at three to four days of age affects the accuracy of pecking, even in dark-reared chicks (Hailman, 1967). Stimulus preference also develops, such that naïve four day old Franklin's Gulls (*L. pipixcan*) respond less well to two-dimensional head models than do hatchlings (Collias & Collias, 1957). The pecking response of five to six day old naïve Laughing Gulls and American Herring Gulls towards two-dimensional head and bill models also differs from that of hatchlings, but the trend is less clear-cut, indicating a loss of specificity in the stimuli that release pecking rather than a directional change in behaviour (Margolis *et al.*, 1987; Alessandro *et al.*, 1989). The chick pecking response diminishes as adult behavioural forms gradually emerge, in concert with the various developmental and motivational stages passed through as chicks grow. For example, aggression towards head models supersedes begging at about a week in age in the Black-headed Gull, a response that then wanes again towards fledging (Groothuis, 1989b).

Tinbergen and Perdeck (1950) themselves used wild-reared chicks for their experiments, which they took from the nest at a young age when the chicks had just dried out after hatching. However, such chicks would have seen their parents, and might have been fed, and as such, the responses recorded might not have been comparable for all individuals, and might not have truly reflected innate pecking behaviour as the authors claimed (for a discussion, see ten Cate, 2009; ten Cate *et al.*, 2009). Subsequent work with incubator hatched chicks has found some deviations in chick behaviour from that described by Tinbergen and Perdeck (1950) (Hailman, 1967; Nyström, 1973; Alessandro *et al.*, 1989).

3.2 EXPERIMENTAL QUESTIONS

The experiments described in this chapter were carried out to address the following questions:

1) Do Lesser Black-backed Gull chicks respond similarly to model heads and real heads, as is the case with Herring Gull chicks (Tinbergen & Perdeck, 1950)?
2) How do Lesser Black-backed Gull chicks respond to modifications of the red spot?
3) Is the pecking response affected by the experimental context, i.e. laying order, time since hatching (chick age), stimulus experience and various correlates of egg and parental quality?

3.3 METHODS

3.3.1 Fieldwork

Fieldwork was carried out during two separate breeding seasons of the Lesser Black-backed Gull in 2006 and 2008 on Flat Holm (section 2.2.1) under licence numbers OTH:SB:02:2006/2008 from the Countryside Council for Wales. All experimental work was in line with the guidelines on the ethical treatment of animals in behavioural research, as set by the Association for the Study of Animal Behaviour.

3.3.1.1 FIELD SEASON 2006

Experimental work required the temporary removal of young from the nest. During 2006, chicks were taken from their parents on the morning of the day of experimentation, and returned in the evening of the same day. Chicks were chosen if they were considered old enough to have dried off after hatching and able coordinate themselves sufficiently well to take part in behavioural tests, but not so old that they would have had extensive experience of feeding and other stimuli that could influence the results. Based on their appearance and their masses, the majority of chicks tested were aged between 12 and 36 hours old, although some were bigger and heavier, and could have been two or even three days old (for growth curves of Lesser Black-backed Gull chicks from the inner Bristol Channel, see Mudge, 1978).

Suitable chicks were taken as they were found in the colony. They were placed individually in numbered bird bags and their parental nest was marked by a numbered, flagged bamboo cane, such that chicks could be returned to the correct nest after testing. Up to twelve chicks were taken from the colony at a time, giving a total of 202 chicks between 20th May and 14th June 2006. At the peak of chick hatching, sufficient numbers of chicks could be found in as little as 15 minutes, but earlier and later in the breeding season this search took up to two hours. Chicks were only taken from the nest when other chicks or eggs were present, to reduce the likelihood of the parents abandoning their nest. No more than one chick was removed per nest to avoid pseudoreplication of chicks within nests (Hurlbert, 1984).

Chicks were carefully transported from the colony to an unheated empty room in Flat Holm's Victorian barracks, where they were placed individually in adjacent compartments (8.5 cm long x 8.5 cm wide x 30.5 cm high) in a cardboard box. They were thus in acoustic contact with their neighbours, but were unable to see them. Each compartment had air holes punched through the sides, and was lined with insulating straw, newspaper and absorbent kitchen towel. The box was wrapped in blankets and covered in a towel. It was heated from below by a hot water bottle, which kept the temperature between 23°C and 27°C, as young chicks can maintain their homoeothermic body temperature when ambient temperature is within this range (Dunn, 1976).

Once collected and installed, chicks were left for approximately two hours before experimenting commenced. This was to allow chicks to build up an appetite, as sated chicks show lower levels of begging behaviour than hungry ones (Impekoven, 1969; Iacovides & Evans, 1998). Chicks were given water (administered from a 0.1 ml transparent syringe) before or during experimentation if dehydrated, but were otherwise not fed or watered until prior to their return to the parental nest, when they were fed to satiation on a mixture of tinned tuna and fish-based cat food. Chicks were frequently used for two different sets of experiments on the same day, as the responses observed were already known not to be those of naïve chicks.

3.3.1.2 FIELD SEASON 2008

The chick selection and husbandry procedure used for the majority of subjects in experiments carried out in 2008 is described in sections 2.3.1 and 2.3.2, whereby pipped eggs were taken from a monitored area of the gull colony and hatched and temporarily reared experimentally. However, towards the end of the field season, insufficient numbers of pipped eggs were available in this area. Thus, a small number of 17 chicks were taken as pipped eggs from nests elsewhere, which were marked with bamboo canes, and then treated according to the same procedures described in section 2.3.2.

3.3.2 Behavioural experiments

3.3.2.1 STANDARD PROTOCOL

Tests were conducted indoors, but in a different room from that in which the eggs/chicks were kept. Experiments were illuminated by natural light from large windows. Chicks were presented with stimuli designed to elicit pecks in a circular rubber tub (45 cm diameter, 17 cm high), covered in a clean plain dark green cloth. This "arena" was approximately twice chick height to minimize the likelihood that subjects would be distracted by landmarks in the room, while the circular shape and plain surface were intended to prevent chicks from being attracted to particular features of the arena, for example corners or different colours.

Chicks were placed in the arena for one minute prior to the start of each test. A stimulus was then held vertically approximately 2 cm front of the subject, with the model's beak or tip pointing downwards, and moved in such as way as to subtend an arc of 5 cm every second, based on the methods described by Tinbergen and Perdeck (1950) and Hailman (1967). Timing commenced when chicks made their first peck at the stimulus, and the number and position of pecks (i.e. pecks to the gonys spot, gape and eye) was counted during the 30 second period thereafter.[24] Pecks directed at objects other than the stimulus, such as the chick's own feet or the ground, were also recorded. A peck was defined as a deliberate, controlled movement towards the stimulus, which resulted in contact with the chick's bill. No distinction was made between pecks where chicks grasped the stimulus and those where they merely touched it. Intervals of approximately 20 minutes, during which chicks were returned to their compartments, were left between the presentation of each stimulus to minimize habituation to the experimental process.

Experiments were carried out by two observers, who took it in turns to time trials and note results, or present the models and count pecks. Contrary to Tinbergen and Perdeck's (1950) methodology, imitation parental mew calls were not used to attract chicks to the stimulus. This was primarily because they were not necessary to elicit the pecking response, but also to avoid confusing the chicks, who might have heard and begun to learn their own parents' calls before they were removed from the nest, even if they were taken before hatching (Impekoven, 1970; 1976).

The colours of the stimuli used were measured with an Ocean Optics CHEM2000-UV-VIS fibre optic spectrophotometer, with an Avantes DH-2000 deuterium (215-400 nm) halogen (360-1700 nm) light source and calibrated with a WS-1 Spectralon diffuse reflectance standard. Twenty adult Lesser Black-backed Gulls were also captured on Flat Holm and their bill measured with the same equipment, to compare the colours of the stimuli with the

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[24] As well as consistency with techniques formerly used (e.g. Tinbergen & Perdeck, 1950; Hailman, 1967), starting the clock at the first peck was judged to be a fairer test of chicks' pecking abilities than commencing timing when the stimulus was first introduced to the arena, as some chicks took longer to notice the stimulus than others.

actual colours found in the wild (Fig. 3.2). Birds were caught on the nest, and were only away from their eggs for approximately half an hour before release. These adults were ringed, and observations showed that they successfully returned to their nests and resumed normal incubation behaviour thereafter.

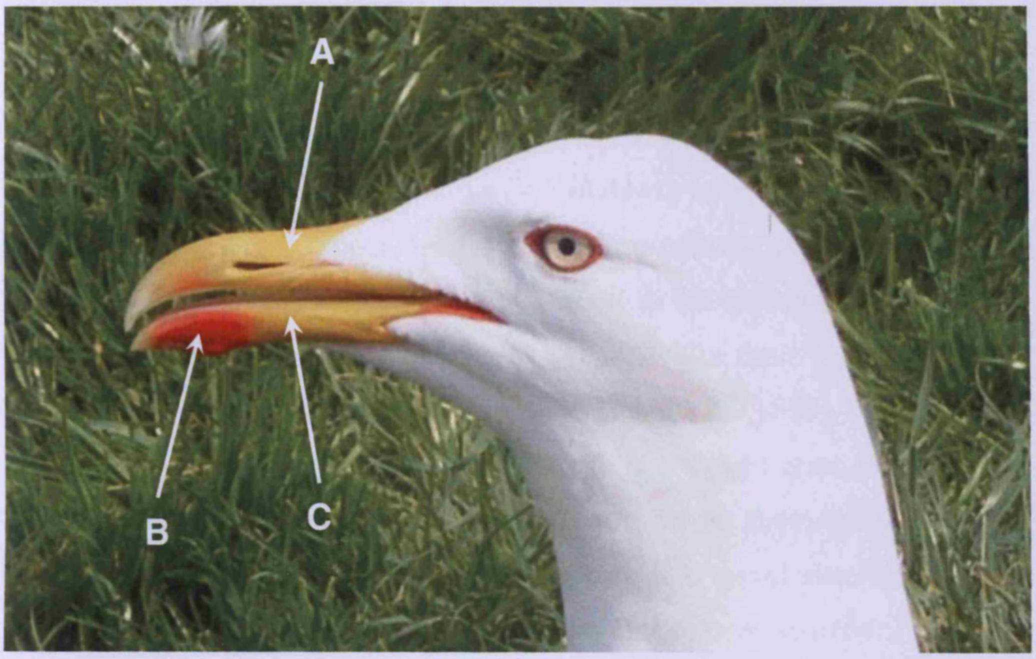

Fig. 3.2. The location of colour measurement of adults captured for comparison of the colours of their bills with those of the stimuli used in behavioural experiments. A – upper mandible, B – gonys spot, C – lower mandible. See also Fig. 3.4.

Experiment 3.1 - Pecking released by real heads and models

Although the approximate size and appearance can be deduced from descriptions, drawing and photographs, the literature produced by Tinbergen and his co-workers (Tinbergen & Perdeck, 1950; Tinbergen, 1953) did not specify the exact dimensions, or accurately quantify the colour,[25] of the stimuli used in their work on the pecking response. Models based on those used by Tinbergen and co-workers were therefore tested to determine

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[25] Tinbergen and co-workers measured colour with the Hering Scale (Tinbergen & Perdeck, 1950). The spectral reflectance of the colours they used has recently been measured by ten Cate *et al.* (2009), and do not closely match those of an adult gull's beak.

whether a response would be elicited from Lesser Black-backed Gull chicks, a species in which chick pecking behaviour had not been previously studied.

Twenty chicks of unknown age and experience (collected from the colony after hatching) were presented with three types of head stimuli on three dates between 20th and 29th May 2006. Three real heads (a different one on each date) from recently deceased (but still in good condition) adult Lesser Black-backed Gulls found in the colony were compared with five card, stick-mounted two-dimensional models of adult heads in profile (gonys spot diameter = 10 mm, bill length = 53 mm, bill depth at gonys = 16.5 mm), and six three-dimensional model heads made from painted polyurethane. The dimensions of the card models were designed to fall within the range found in the wild (Malling Olsen & Larsson, 2004), while their appearance was based on models used by Tinbergen & Perdeck (1950). The three-dimensional models were cast from the head of a dead Lesser Black-backed Gull. On each day, half the chicks were presented with the natural head first, followed by the polyurethane model and finally the two-dimensional model. The other half of the cohort was offered the heads in reverse order.[26]

Experiment 3.2 - Determining optimum gonys spot size

Chicks were tested to see if they responded preferentially to gonys spots of a particular size. The stimuli were a series of stick-mounted two-dimensional card models, identical to those used in experiment 3.1 except for modifications to the gonys spot. These were presented to 38 chicks of unknown age (collected from the parental nest post-hatching) on five different dates between 26th May and 6th June 2006. The "Small" model had a 5 mm diameter spot, the "Medium" model a 10 mm diameter spot, and the

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[26] This method of sequencing the stimuli was chosen for all experiments carried out in 2006, such that the stimulus presentation order could be entered as a known variable in the models used for statistical analysis. However, this meant that the same stimuli were always in the middle of the sequence, and thus always subject to the same degree of chick habituation. Therefore, this ordering technique was abandoned after 2006, with a random stimulus presentation order adopted for all experiments conducted in 2007, 2008 and 2009.

"Large" model a spot diameter of 15 mm. A "Diffuse" model was also used, with a faded 10 mm diameter spot meant to represent the imprecisely defined border of this bill feature often seen in nature, and there was a "Target" model with a 5 mm diameter spot surrounded by a 10 mm diameter red circle, based on Tinbergen & Perdeck's (1950) "supernormal spot" (which they did not mount on a head model, but instead presented on a piece of rectangular card). On each day, half the chicks were presented with the stimuli in the order Small, Medium, Large, Diffuse, Target, while the other half were presented with the stimuli in the opposite sequence.

Experiment 3.3 - Ultraviolet reflectance of the gonys spot

Tinbergen and co-workers' original work on the pecking response was conducted before it was known that several avian species possess photoreceptors sensitive in the ultraviolet (UV) range of the spectrum (Hart, 2001). UV-sensitive photoreceptors have been found in gulls (Ödeen & Håstad, 2003), where they are thought to assist in terrestrial foraging (Håstad *et al.*, 2005). This set of trials therefore tested whether altering the UV reflectance of the gonys spot would affect the nature of the pecking response. UV reflective orange bill spots are thought to affect social behaviour in penguins (Jouventin *et al.*, 2005). Three heads of recently deceased adult Lesser Black-backed Gulls were presented to sixteen chicks of unknown age (taken from the parental nest after hatching) on 23rd and 24th May 2006. The UV reflectance of the gonys spot was altered on two of these heads; one with sun cream which enhanced the level of reflectance (UV+), while the other was painted with a shade of red which did not reflect in the UV (UV-) (Fig. 3.7). Similar methods of altering colour, and specifically UV reflectance, have been used successfully in other studies of birds, on both plumage and integument (e.g. Arnold *et al.*, 2002; Korsten *et al.*, 2007; Morales *et al.*, 2009) An unaltered, control head was also used (Control). On each day, half the chicks were presented with the stimuli in the order UV+, Control, UV-, while the other half were presented with the stimuli in the opposite sequence.

Experiment 3.4 - Response to scrambled beak features

Young chicks normally aim pecks at the red spot on their parents' bills despite the presence of other prominent areas of red on the adult heads, notably at the gape and orbital ring. Tinbergen and Perdeck (1950) reported a number of pecks to the eye, while ten Cate *et al.* (2009) found that 6% of pecks to their stimuli were directed away from the gonys spot. The gape colour and elongated shape of the gape suggest it might be attractive to chicks because it shares these features with the superstimulus (SS) (see section 4.1). Older chicks and courting females are known to direct pecks to this region (Brown, 1967c; Velando, 2004). To this end, the gape and spot were scrambled or removed on particular models.

This experiment was carried out on nine naïve (incubator-hatched) chicks on 15th June 2008. Chicks were between 21 and 40.3 hours old at the time the experiment commenced, with a mean age of 26.4 hours. Chicks' reactions to seven different stimuli were tested. The Control was a two-dimensional stick-mounted card model of an adult Lesser Black-backed Gull head in profile (see experiment 3.1). Chicks were also presented with a model without the gape (SnoG), one without the spot (GnoS), one with the spot moved to the position in which the gape is normally found (SinG), one in which the gape was moved into the gonys spot position (GinS), and one in which the spot and gape were reversed, such that the gape was at the gonys and the spot at the gape (GxS) (Fig. 3.3). A 3 mm diameter SS (see section 4.1), with three 2 mm wide white stripes 2 mm apart, 16 mm from the tip, was added to this series of stimuli, and was designed to correspond to the SS Tinbergen and Perdeck (1950) used, although its dimensions were optimised during experiments carried out during 2006 (experiments 4.2a and 4.2b). To help minimize pseudoreplication of stimuli (Kroodsma, 1989; Ruxton & Colegrave, 2006), six different replicates of each stimulus were available, and the choice of replicate selected at random for each trial by rolling a die.[27] The

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[27] There was still some pseudoreplication of stimuli, as the number of chicks exceeded the number of replicate stimuli.

order of stimulus presentation for each chick was also randomised in the same fashion.

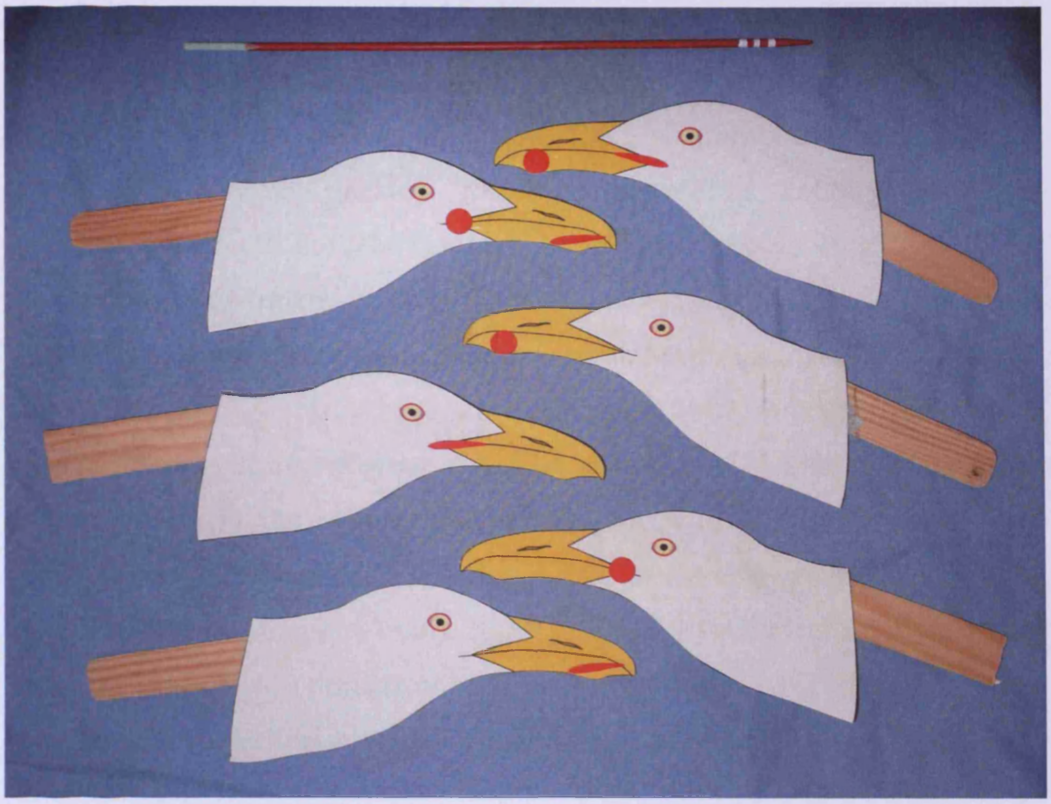

Fig. 3.3. Examples of the stimuli used in experiment 3.4. Top to bottom: SS, Control, GxS, SnoG, GnoS, SinG, GinS.

Experiment 3.5 - Effect of stimulus experience on the pecking response

The Control stimulus was used in all sets of experiments carried out in 2008, allowing examination of the possible effect of the type of experiment being carried out on the chick pecking response. The pecking rate to the Control was thus extracted for 85 naïve (incubator-hatched) chicks taking part in experiment 4.1 (addressing Tinbergen and Perdeck's (1950) hypothesis about the adaptive significance of the supernormal pecking response), experiments 4.2c and 4.2d (examining the role of individual elements of the SS) and experiment 5.2 (looking at the addition of "food" items at the end of the bill tips).[28] These tests took place on 13 separate dates between 21st May and 14th June with chicks aged between 3.8 and 48.3 hours old (mean age, 26.1 hours).

3.3.3 Statistical treatment

All results were analyzed in R version 2.8.1 (R Core Development Team, 2008). The additional package "nlme" (Pinheiro *et al.*, 2008) was used for linear mixed-effects models (LMMs), and "lme4" (Bates *et al.*, 2008) for generalized linear mixed models (GLMMs), while *post-hoc* multiple pairwise comparisons were undertaken with the "multcomp" package (Hothorn *et al.*, 2008). The package "MASS" (Venables & Ripley, 2002) was used for Box-Cox transformations of non-normal response variables. Calculation of distances between nests in the colony was carried out with the "spatstat" package (Baddeley & Turner, 2005). Graphical figures were prepared in R version 2.8.1 (R Core Development Team, 2008) and GraphPad Prism 2.01 (GraphPad Software Inc., 1996). Statistical tests were two-tailed, with the significance level set at 0.05. Values are given as arithmetic means ± SE.

Data from the behavioural experiments were analyzed using a series of general linear models (after the approaches described in Grafen & Hails, 2002, and Crawley, 2007), LMMs (Pinheiro & Bates, 2000) and GLMMs (Bolker *et al.*, 2008). Linear models were used when the response variable was continuous, provided this variable passed the Shapiro-Wilk normality test and checks of the minimum adequate model showed that assumptions were not violated (e.g. homogeneity of variance) (Pinheiro & Bates, 2000; Grafen & Hails, 2002; Crawley, 2007). If this was not the case, transformations were carried out, and linear modelling proceeded. In all experiments except experiment 3.2 (spot size), the continuous response variables could be normalized in this fashion. In experiment 3.2, a GLMM with a poisson error was fitted.

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[28] The experiment on scrambling beak features (experiment 3.4) was excluded from these analyses as the sample size (nine chicks) was much smaller than for the other sets (between 22 and 31 chicks).

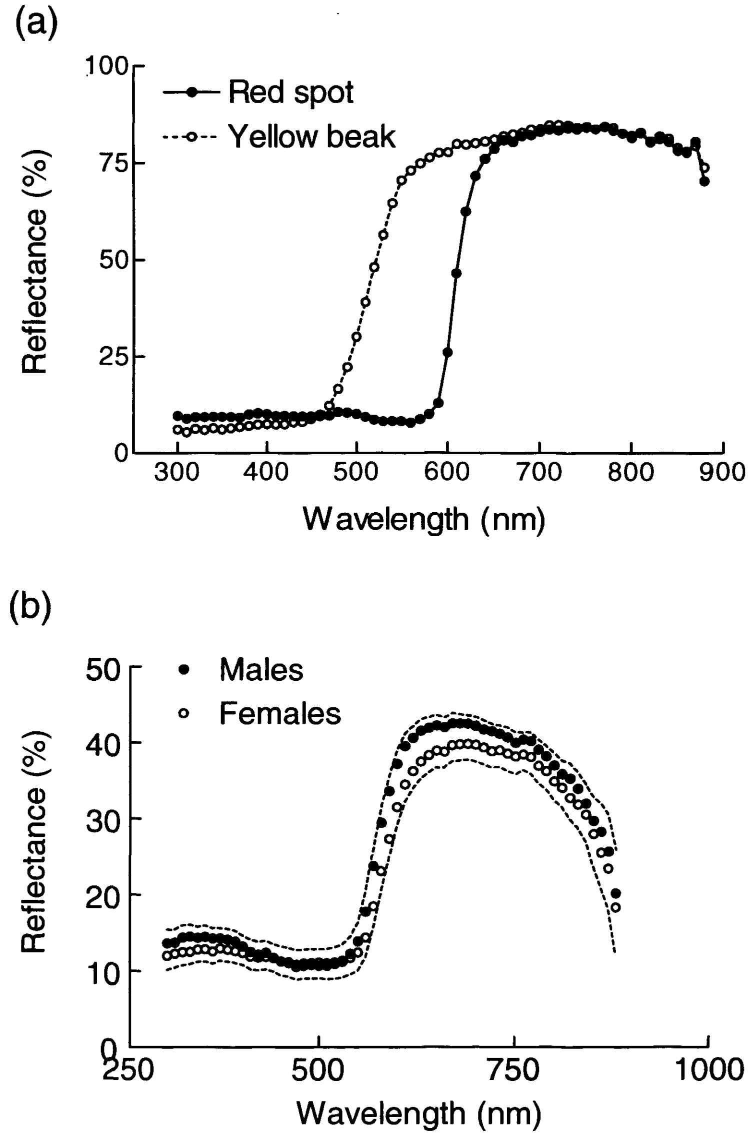
Model simplification proceeded via stepwise deletion of non-significant terms (Crawley, 2007), with comparison of the p-value of the likelihood ratio statistic and the Aikaike Information Criterion (AIC) at each step (Pinheiro & Bates, 2000). *Post-hoc* multiple pairwise comparisons of the different levels of significant categorical explanatory variables were undertaken using the Tukey Honest Significant Difference method.

In all models, the response variable was the total number of pecks per 30 second trial, including those aimed away from the model, such as to a chick's own feet. As chicks were often subject to repeated trials with several different stimuli within each experiment, chick identity was fitted as a random effect in all models except those for experiment 3.5, where repeated measures were not made. Explanatory variables found in all models were stimulus type, order of stimulus presentation and the date on which the experiment was carried out. In models based on 2006 data, chick mass was included as a proxy for age. For 2008 data, chick age in hours post-hatching at the start of each experiment was included, as was the volume of the egg from which each chick had hatched. Chick laying order was also known for 2008 chicks, as were two measures of parental quality: the distance of the parents' nest to its nearest neighbour and nest quality measured on a five point scale (Fig. 2.8). The week in which an egg was laid was also included. In experiment 3.5, the nature of the experiment carried out (e.g. "Food" for experiment 5.2) was also included as an explanatory variable. Interactions were only fitted if they were thought to be informative and biologically meaningful to help reduce the potential problem of multiplicity of p-values (Grafen & Hails, 2002). Therefore, no interactions of a higher order than two-way were included.

3.4 RESULTS

Experiment 3.1 - Pecking released by real heads and models

Stimulus type did not have a significant effect on the rate of chick pecking (LMM, $F_{2,30}$ = 1.45, p = 0.2499), with 17.29 ± 1.97 pecks for the two dimensional head, 17.06 ± 2.71 pecks for the real head, and 14.41 ± 1.99 pecks for the polyurethane head. This is despite the spectral reflectance of the colours of the models' bills being quite different from those of real heads (Fig. 3.4).



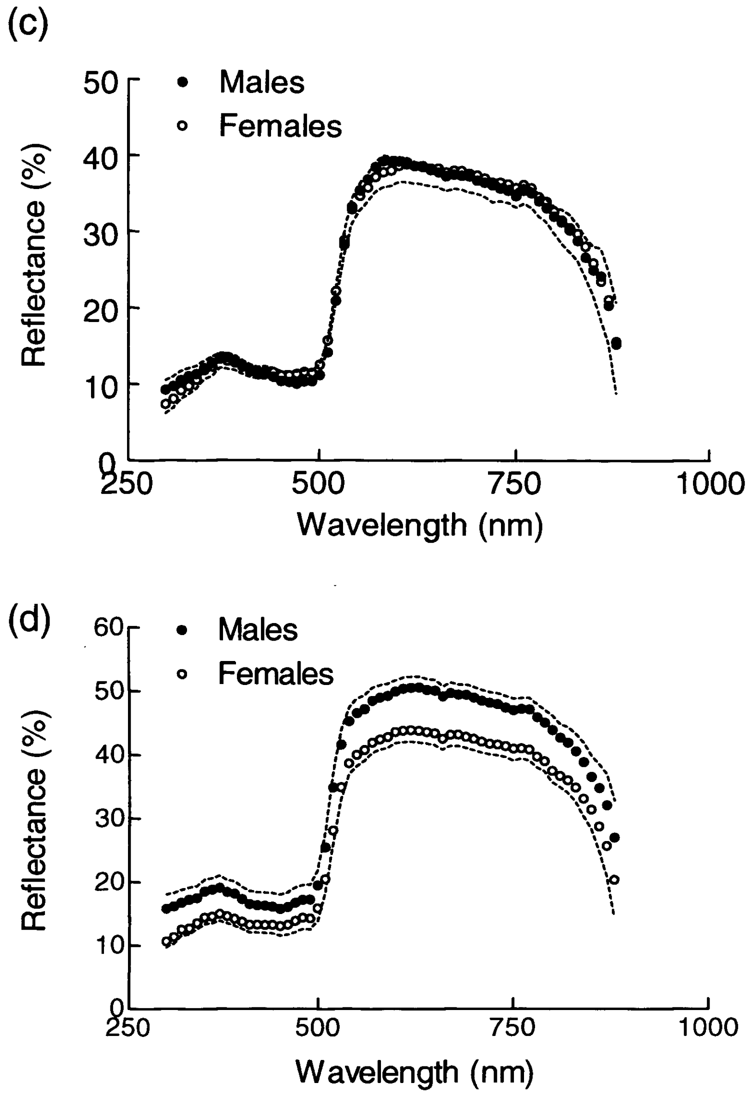


Fig. 3.4. Spectral reflectance of the bill colours of models and breeding adult Lesser Black-backed Gulls: (a) two-dimensional model, (b) adult gonys spot, (c) adult upper mandible, (d) adult lower mandible. Graphs of adult bills show mean for each sex ± S. E.

Chick mass, experimental date and stimulus presentation order were also insignificant. However, there was a significant interaction between stimulus type and chick mass (LMM, $F_{2,30} = 10.31$, $p = 0.0004$). Fig. 3.5 shows that the number of pecks given to real adult heads increased with increasing chick mass, with the same but shallower relationship for the three-dimensional model, and the inverse relationship for the two-dimensional model.

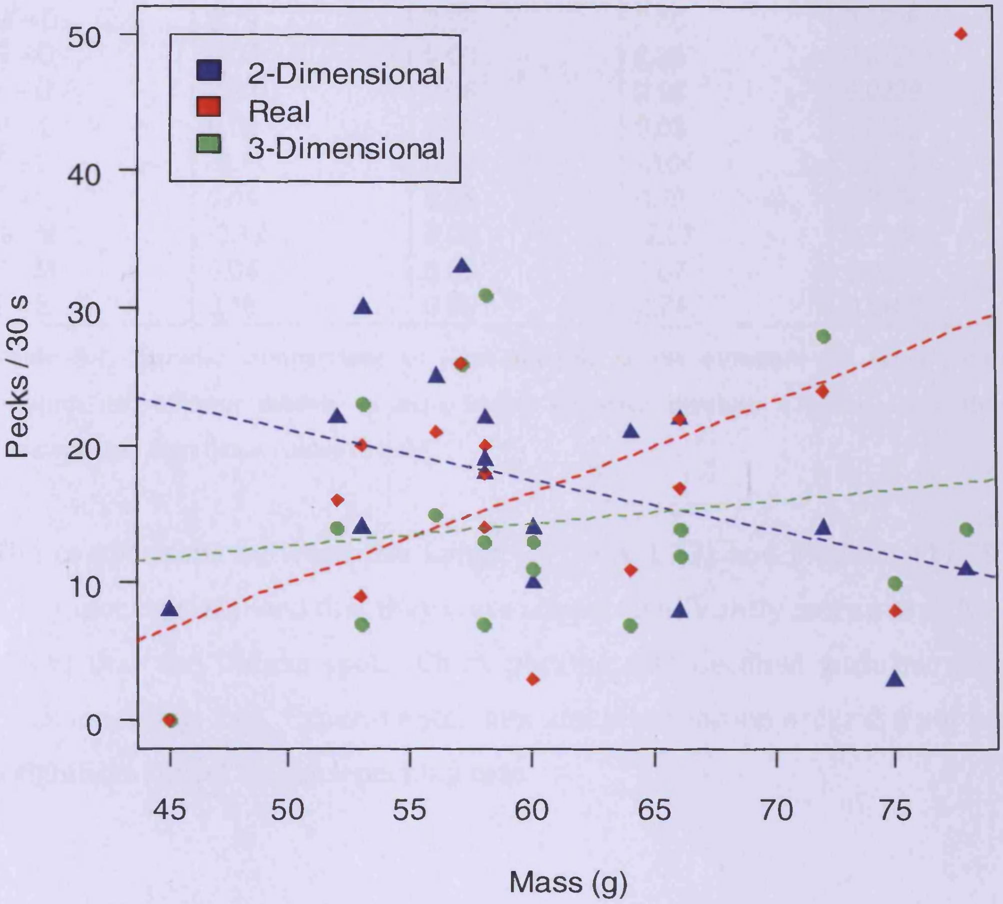


Fig. 3.5 The relationship between chick mass, stimulus type and rate of pecking in experiment 3.1. Chicks responded better to more realistic heads as they aged, and less well to less realistic heads.

Experiment 3.2 – Determining optimum gonys spot size

Stimulus type had a significant effect on the rate of chick pecking (GLMM, $z \geq 2.51$, $p \leq 0.0118$), as did chick mass (GLMM, $z = -2.31$, $p = 0.0210$). Multiple comparisons showed that the Target spot elicited significantly more pecks (18.45 ± 1.59) than either the Diffuse (14.39 ± 1.72) or the Small (15.84 ± 1.28) spot sizes (Table 3.1).

Comparison	Estimate	S.E.	z	*p*
L – D	0.19	0.08	2.48	0.0933
M – D	0.19	0.08	2.50	0.0888
S – D	0.07	0.08	0.96	0.8725
T – D	0.23	0.08	2.99	**0.0228**
M – L	0.00	0.05	0.03	1.0000
S – L	-0.11	0.06	-2.04	0.2412
T – L	0.04	0.05	0.70	0.9554
S – M	-0.12	0.06	-2.07	0.2288
T – M	0.04	0.05	0.67	0.9613
T – S	0.15	0.06	2.74	**0.0469**

Table 3.1. Pairwise comparisons of least squares means estimates for chick pecking response to different models in experiment 3.2, with *p*-values adjusted for multiple comparisons. Significant values in bold.

The comparisons between the Large (17.76 ± 1.27) and Medium (17.79 ± 1.42) spot sizes showed that they were almost significantly more attractive to chicks than the Diffuse spot. Chick pecking rate declined with increasing chick mass (Fig. 3.6). Experimental date and presentation order did not have a significant effect on chick pecking rate.

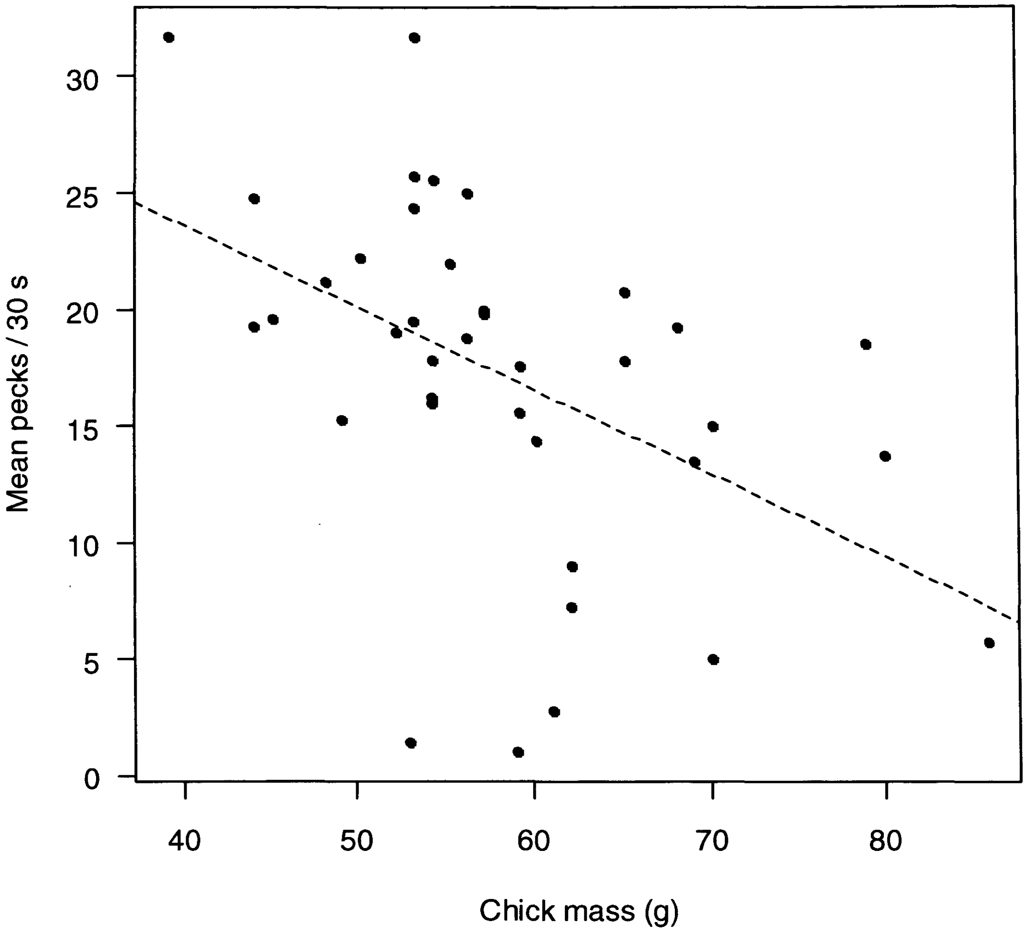


Fig. 3.6. The relationship between chick mass and rate of pecking in experiment 3.2. Pecking response (y-axis = mean response per chick to all stimuli) declines with increasing chick mass.

Experiment 3.3 - Ultraviolet reflectance of the gonys spot

The treatments used successfully altered the UV reflectance of the gonys spot (Fig. 3.7).

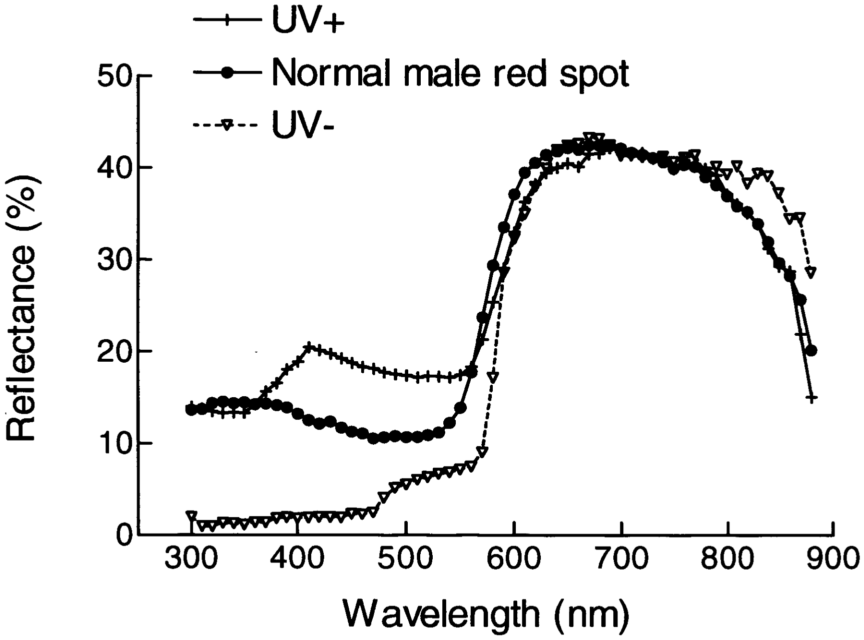


Fig. 3.7. The effect of experimental treatments used in experiment 3.3 on gonys spot spectral reflectance. The suncream treatment successfully enhanced spot UV reflectance, while the paint significantly reduced it.

Stimulus type had a significant effect on chick pecking rates (LMM, $F_{2,28}$ = 4.39, p = 0.0220), as did experimental date (LMM, $F_{1,14}$ = 6.93, p = 0.0197). Closer inspection revealed that both the UV reduced (22.31 ± 3.34 pecks per 30 seconds) (LMM, t_{28} = 3.491, p = 0.0016) and the UV enhanced (22.31 ± 3.17) heads (t_{28} = 3.81, p = 0.0007) elicited a significantly greater rate of pecking than did the unaltered head (16.56 ± 2.35). Additionally, there was a significant interaction between experimental date and stimulus type (LMM, $F_{2,28}$ = 4.81, p = 0.0160), with an increase in pecking towards UV altered stimuli on 23rd, but a weak trend in the opposite direction on 24th (Fig. 3.8). Overall, mean pecking rates on 24th May (12.89 ± 2.73) were approximately half those on than on 23rd May (24.90 ± 1.82). There was no significant effect of chick mass or order of stimulus presentation.

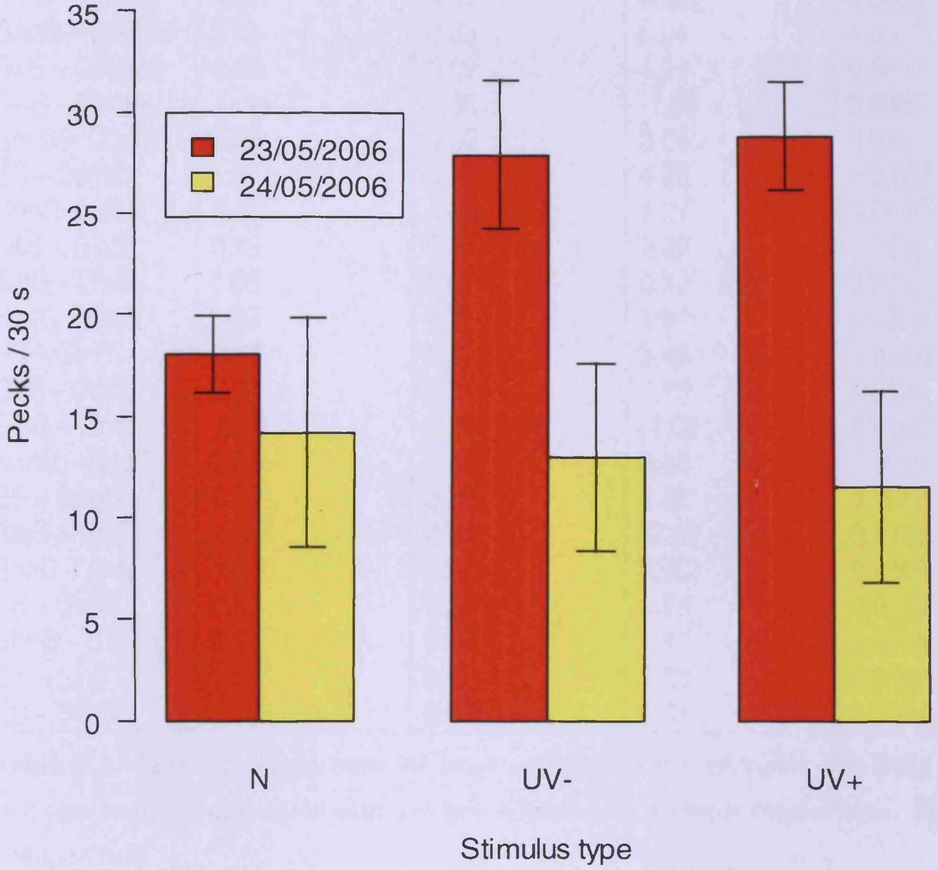


Fig. 3.8. The relationship between gonys spot reflectance and chick pecking rate in experiment 3.3 on two consecutive dates. Chick pecking rate was higher towards gonys spots with manipulated UV reflectance than to the unaltered bill on 23rd May 2006, but the opposite effect was seen on 24th May 2006.

Experiment 3.4 - Response to scrambled beak features

Only stimulus type (LMM, $F_{6,41} = 8.62$, $p < 0.0001$) and stimulus presentation order (LMM, $F_{6,41} = 3.01$, $p = 0.0156$) had a significant effect on the total number of pecks delivered to each model. The order effect was indicative of habituation with repeated exposure to stimuli. Pairwise comparisons of the stimulus type effect (Table 3.2) showed that the SS elicited a significantly greater number of pecks than any of the other stimuli types, none of which was significantly different from any of the others (Fig. 3.9).

Comparison	Estimate	S.E.	z	*p*
GinS – Control	-0.41	0.32	-1.28	0.8633
GnoS – Control	0.01	0.33	0.04	1.0000
GxS – Control	0.39	0.32	1.21	0.8897
SinG – Control	-0.34	0.32	-1.08	0.9355
SnoG – Control	0.22	0.32	0.69	0.9931
SS – Control	1.34	0.32	4.20	**< 0.001**
GnoS – GinS	0.42	0.33	1.27	0.8639
GxS – GinS	0.79	0.32	2.49	0.1637
SinG – GinS	0.06	0.32	0.20	0.9999
SnoG – GinS	0.63	0.32	1.97	0.4360
SS – GinS	1.74	0.32	5.48	**< 0.001**
GxS – GnoS	0.37	0.33	1.13	0.9194
SinG – GnoS	-0.36	0.33	-1.08	0.9340
SnoG – GnoS	0.21	0.33	0.63	0.9960
SS – GnoS	1.32	0.33	4.02	**0.0013**
SinG – GxS	-0.73	0.32	-2.29	0.2498
SnoG – GxS	-0.17	0.32	-0.52	0.9986
SS – GxS	0.95	0.32	2.99	**0.0442**
SnoG – SinG	0.56	0.32	1.77	0.5711
SS – SinG	1.68	0.32	5.28	**< 0.001**
SS – SnoG	1.12	0.32	3.51	**0.0081**

Table 3.2. Pairwise comparisons of least squares means estimates for chick pecking response to different models, with *p*-values adjusted for multiple comparisons. Significant values in bold.

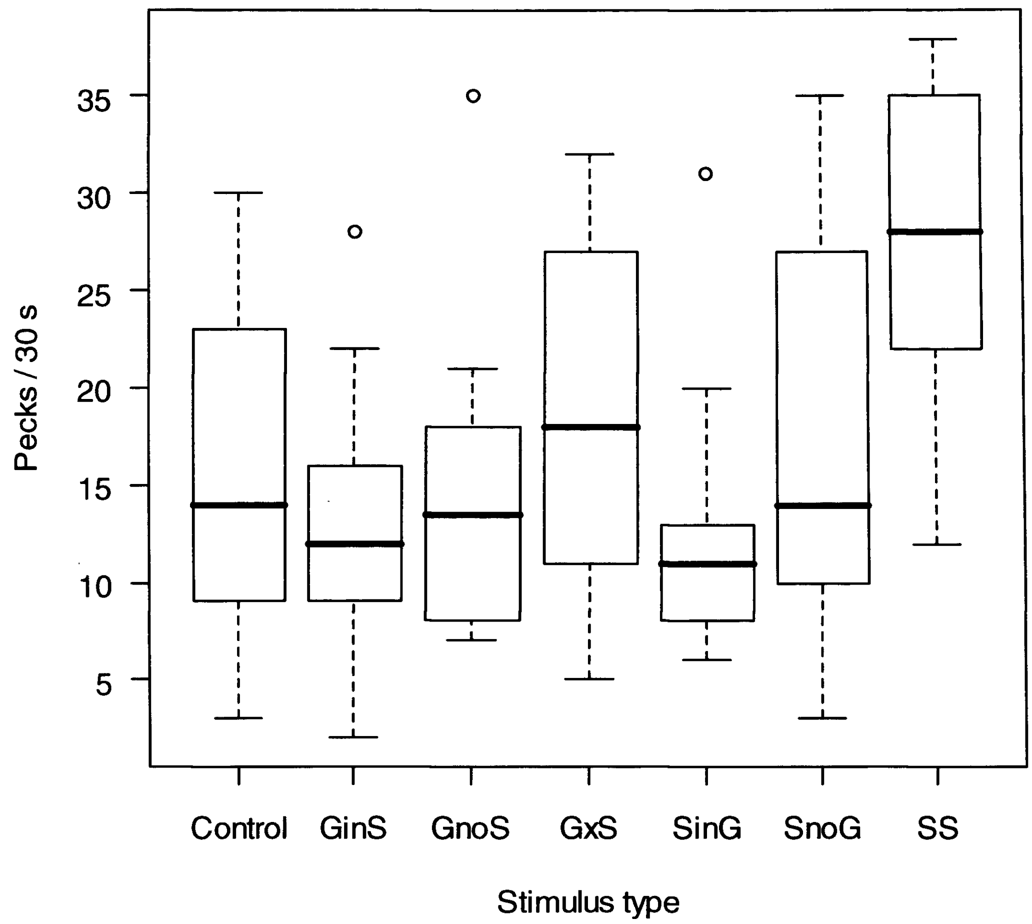


Fig. 3.9. The relationship between stimulus type and chick pecking rate in experiment 3.4. The SS elicited a significantly stronger effect on chick pecking than any of the other stimuli, which were not significantly different from each other.

Experiment 3.5 - Effect of stimulus experience on the pecking response

After model simplification, only chick age (ANOVA, $F_{1,80} = 6.31$, $p = 0.0140$) and the type of experiment conducted (ANOVA, $F_{3,80} = 8.85$, $p < 0.0001$) were significant predictors of chick pecking. The overall explanatory power of the model was low, with an adjusted R^2 of 25.57%. The age effect showed that the rate of pecking increased as chicks got older (Fig. 3.10). Tukey comparisons of the experimental effect (Fig. 3.11) showed that the chicks taking part in experiment 4.2d, in which one element of the SS was removed from various beak models, pecked significantly more towards the Control (20.09 ± 1.55) than did chicks taking part in experiment 4.2c, where only a single element of the SS was added to beak models (10.41 ± 1.19). Chicks taking part in experiment 4.1, examining the ventral view hypothesis, also pecked at a greater rate towards the Control (17.13 ± 1.16) than chicks taking part in experiment 4.2c (Table 3.3).

Comparison	Estimate	S.E.	t	*p*
Single - Food	-4.89	2.53	-1.93	0.2201
Three - Food	4.79	2.53	1.89	0.2363
Ventral - Food	1.83	2.42	0.76	0.8714
Three - Single	9.68	2.00	4.83	**< 0.0001**
Ventral - Single	6.72	1.85	3.63	**0.0026**
Ventral - Three	-2.96	1.85	-1.60	0.3803

Table 3.3. Pairwise comparisons of least squares means estimates for chick pecking response to Control stimulus in the context of different experiments, with *p*-values adjusted for multiple comparisons. Food = experiment 5.2, Single = experiment 4.2c, Three = experiment 4.2d, Ventral = experiment 4.1. Significant values in bold.

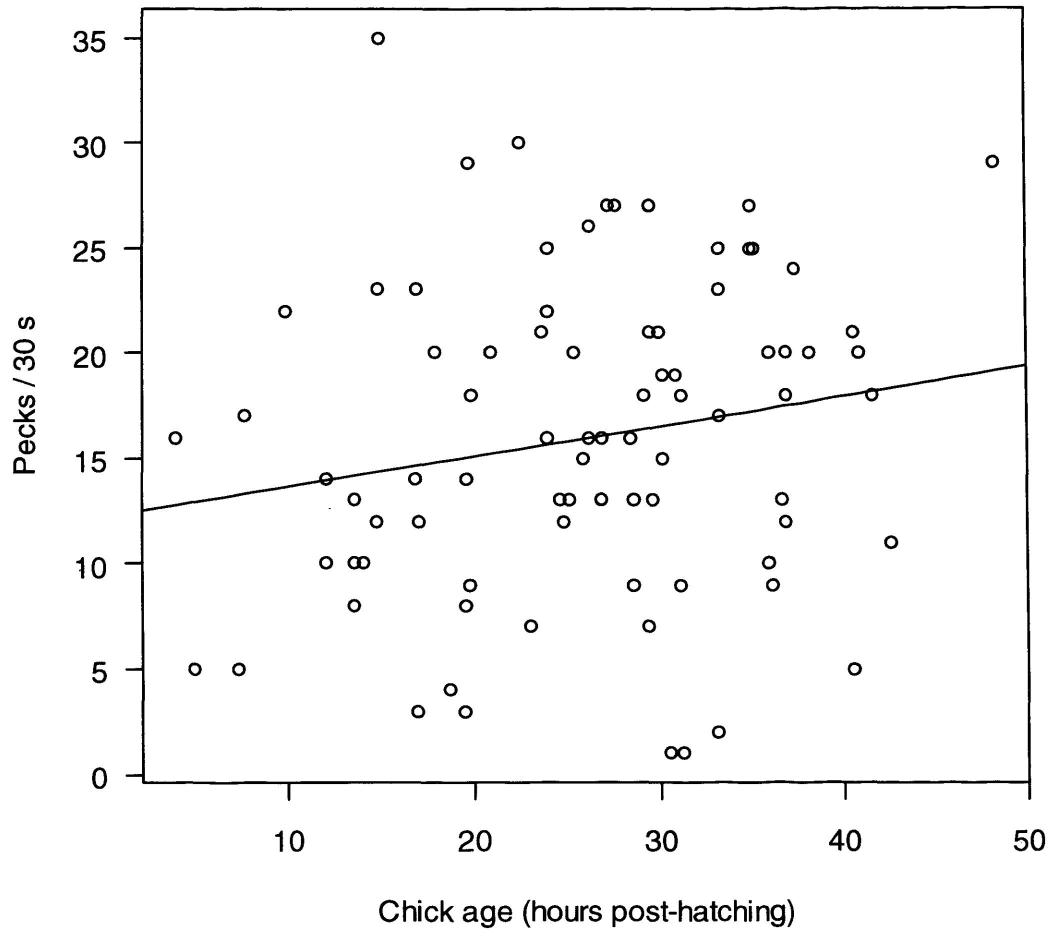


Fig. 3.10. The relationship between chick pecking rate and age. Chicks' rate of pecking increased significantly with age.

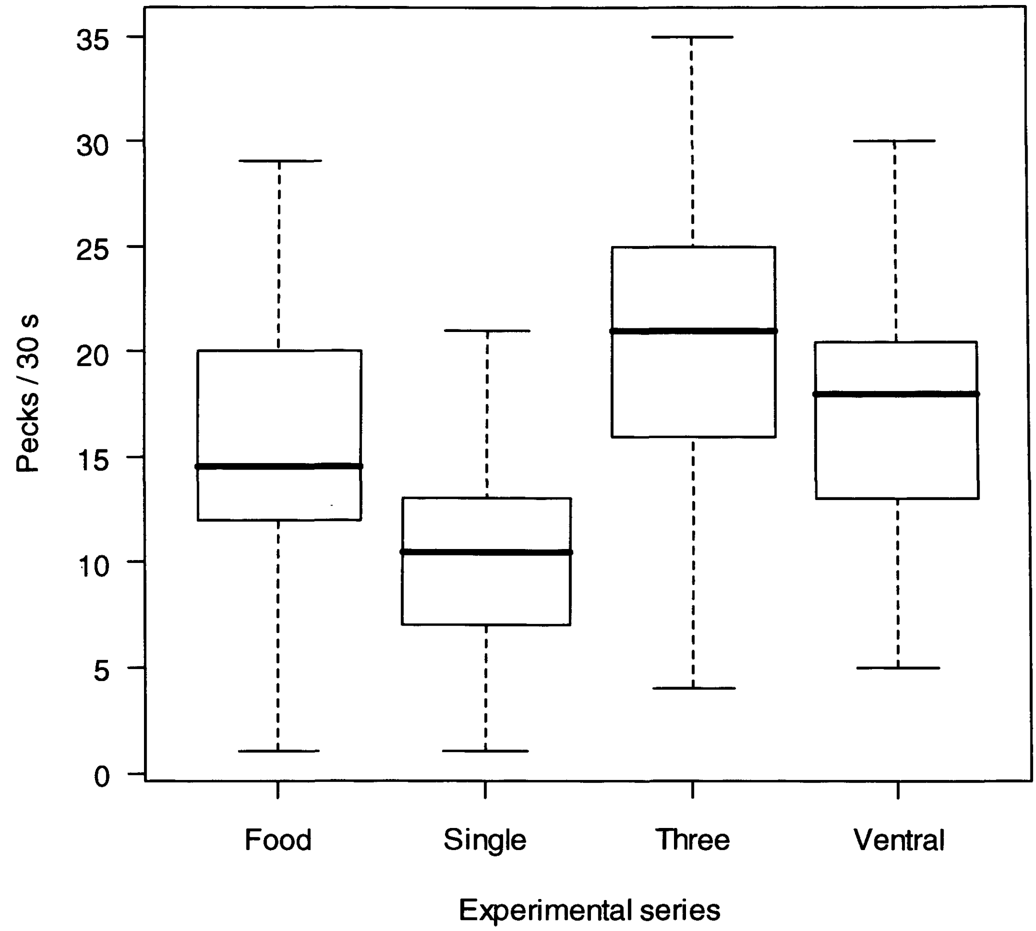


Fig. 3.11. The relationship between chicks' experience and pecking responses in experiment 3.5. Chicks' pecking to the Control was affected by the other stimuli they were exposed to during the course of the experiment they took part in. Food = experiment 5.2, Single = experiment 4.2c, Three = experiment 4.2d, Ventral = experiment 4.1.

3.5 DISCUSSION

The findings of this chapter shed some light on the details and subtleties of the chick pecking response in Lesser Black-backed Gulls. It appears that immediately post-hatching, pecking behaviour is triggered more effectively by conspicuous stimulus features, for example the gonys spot, than by more complex properties such as whether or not the stimulus concerned is three-dimensional. Chicks are sensitive to changes in the size, form and colour of the gonys spot, such that their behaviour differs with adjustment of this feature. Nevertheless they respond well to a range of stimuli, even when the spot is absent, or when the stimulus colours are not closely matched with those found in the wild. The chick pecking response is also altered by exposure to other stimuli.

3.5.1 The role of bill and head features in the pecking response

The first finding of note indicated that, as Tinbergen and Perdeck (1950) inferred for Herring Gulls, using models of an adult Lesser Black-backed Gull head is a viable way of testing a chick's pecking response. Not only did chicks respond well to all stimuli, their pecking rate was not significantly different to either a two-dimensional or a three-dimensional representation of a head than it was to a real adult head, indicating that chicks of this age cannot yet detect this type of difference. They were also not sensitive to the deviations in the bill colour of the models from that of a real adult head. The red spot on the two-dimensional card model rose steeply in the red range of the spectrum between around 600 nm and 650 nm before plateauing at its maximum reflectance up to around 900 nm. The reflectance of the actual adult spot, in contrast, rose at shorter wavelengths, from around 550 nm, to reach a peak at around 650 nm, and dropped off again between around 750 nm and 900 nm. Similarly, the yellow of the two-dimensional model increased sharply at around 500 nm and remained high until about 900 nm, while the adult bill's yellow peaked between about 550 nm and 750 nm (Fig. 3.2).

Again echoing Tinbergen and Perdeck's (1950) results, manipulating the gonys spot by adding a ring around it significantly increased its attractiveness. The addition of such a ring may have increased the spot's attractiveness by giving it some resemblance to the most powerful feature of the SS, the stripes (experiments 4.2c and 5.2d). The mean number of pecks to this stimulus was not, however, as high as the mean number given to the SS in either experiment 3.4, or those detailed in Chapters 4 and 5 (experiments 4.1, 4.2c, 4.2d, 5.2). The fact that an additional coloured region (an outer ring in this case) elicits a significantly enhanced chick response might indicate how such an innovation could become fixed in the adult population, if its serves to facilitate chick feeding and hence survival. Indeed, breeding adults of certain species closely related to the Lesser Black-backed Gull, including the California Gull (*L. californicus*), and the Armenian Gull (*L. armenicus*) have a (black) stripe adjacent to the gonys spot (Malling Olsen & Larsson, 2004), which produces an effect a little like the Target spot. A parsimonious approach to a recent phylogeny (that of Pons *et al.*, 2005) shows that these stripes evolved after the spots (Ferns & Ross-Smith, 2009), suggesting that they are selectively advantageous additions to the bill. Other more distantly related species, such as the Great Black-headed Gull (*Ichthyaetus ichthyaetus*), also have bill stripes associated with larger patches of a different colour (Olsen & Larsson, 2004), indicating convergent evolution of these bill features. It may not, however, be adaptive for adults to have bill markings that supernormally stimulate chick pecking to too great a degree, as the effort of such pecking could prove energetically costly for chicks, and chicks must be able to switch their attention from pecking at the bill to pecking at food.

Small spots and those without a sharply defined boundary were less effective at eliciting pecks. The spot without a sharply defined border was designed to exemplify some of the gonys spots found on breeding adults in the wild (Fig. 3.12). The ineffectiveness of models with this type of spot suggests that there could be selection on adults to have neat, prominent spots. The spot without the defined border was also a more diffuse colour than the other spots, which is also representative of certain spots found in the wild (Fig. 3.12). This decrease in colour intensity could also have contributed to this model's relative unattractiveness to chicks. It appears that spots in the Medium and Large size range are equally effective at eliciting a response from the chicks. Such behaviour is adaptive, as both these sizes are within the range normally seen in breeding adults in the wild, and chicks would thus need to respond to them just as strongly to induce food regurgitation by their parents. The effect of differences in spot size and colour intensity on chick pecking behaviour is reminiscent of a recent study showing that experimental manipulation of spot size affects an individual's parental effort and that of its partner in

Yellow-legged Gulls (Morales *et al.*, 2009). As gonys spot size and colour intensity have also been found to be honest signals of phenotypic quality in three different species of large white-headed gull (Blount *et al.*, 2002; Kristiansen *et al.*, 2006; Pérez *et al.*, 2008), the results of these studies together are thus complementary in underlining the gonys spot's importance as a social signal in gulls, affecting both sexual and parent-offspring communication.

Fig. 3.12. A range of gonys spot sizes and colour intensities is found in the wild: (a) "low quality" spot (small size, ill-defined border, pale red), (b) "intermediate quality" spot (brighter, better defined border, larger size), (c) "high quality" spot (large, bright red, well defined). All photos are of breeding adults on Flat Holm, May 2008.

The results of experiment 3.3 in which UV reflectance was manipulated were equivocal. It appeared that chicks increased their rate of pecking towards both the UV enhanced and UV reduced heads, indicating that they were responding simply to the novelty of these heads' unusual gonys spots. Similar responses to atypical stimuli have been reported in Laughing Gull chicks (Griswold *et al.*, 1995). However, this trend was not found on the second of the two dates on which this experiment was carried out, when the pecking rate to all stimuli had also generally decreased. This suggests that these results may be an artefact of the stimuli used. It was not possible to obtain enough heads to have a range of stimuli, or new stimuli from one day to the next, such that the responses observed may have been a consequence of the three particular heads used (Ruxton & Colegrave, 2006). The decline in pecking rate between the first and second day, and the absence of an enhanced response to the modified spots on the second, may have been a consequence of some deterioration in the condition of the heads.

3.5.2 Effect of other factors on the pecking response

The experiments carried out in 2006 used wild-reared chicks that would have had some experience with their parents and hence begun to learn their features. In accordance with this, a significant effect of chick mass, a proxy for age, was found in two of the experiments carried out. In the tests comparing the use of different model types and real heads (experiment 3.1), there was a significant interaction between stimulus type and chick mass, with the trend indicating that two-dimensional models are attractive to young chicks, but this decreases as they age, while simultaneously, the pecking rate at more realistic three-dimensional models and real heads increases. The two-dimensional models might have caught the young chicks' attention, because the sharply defined and high contrast features might have been easier for the hatchling visual system to detect than the more complex characteristics of three-dimensional stimuli. It is also likely, however, that older chicks responded better to more realistic stimuli, because they had had more extensive exposure to their parents at the nest and thus found the stimuli they recognized as resembling their parents the most attractive (Conover & Miller, 1981). The finding that pecking declined as chicks got heavier in experiment 3.2, manipulating spot size, is in accordance with this idea.

In experiment 3.5, carried out with naïve chicks in 2008, age had a significant effect on chicks' responses towards the Control stimulus, with the pecking rate increasing as chicks got older. This was probably due to improved motor coordination of chicks as they aged (Hailman, 1967). Increased motivation to peck through hunger may have also played a part, although newly hatched Lesser Black-backed Gull chicks have four days' worth of yolk reserves (Hario, 2004), and all chicks were much younger than this at the time of testing. Parents do not feed their chicks in the wild until several hours post-hatching (Tinbergen & Perdeck, 1950; personal observation).

There was a significant overall effect of the type of experiment carried out on the rate of pecking at the Control. The only significant difference was between pecks to the Control in the tests designed to assess the effects of individual elements of the SS (experiments 4.2c and 4.2d). In the experiment where a single element of the SS was added to four different models based on the Control (experiment 4.2c), chicks' response to the Control itself was significantly lower than in tests where a single element of the SS was removed from four models based on the Control (experiment 4.2d), with the pecking rate towards the Control in latter approximately double that of the former. This could be because chicks in the trials with five of the six stimuli encountered bearing at least three elements of the SS, had their general level of pecking heightened by such highly attractive stimuli.

Overall, results indicate that chicks respond best to well-defined gonys spots beyond a particular size threshold. It appears that chicks hatch with an innate flexibility in the range of stimuli to which they respond, such that deviations from the optimal stimulus can still effectively induce pecks. This is likely to be adaptive to chicks that hatch from parents with smaller, less intensely coloured spots, while the lack of a specific neural "image" necessary to release pecks might also allow chicks to adapt their behaviour to the distinguishing physical features of their parents. Chicks' pecking behaviour seems to be rapidly attuned to their experience, which is also probably adaptive for learning quickly to identify their parents, the appearance of food items, and the characteristics of their natal territory.

Chapter 4

Experimental investigation of the adaptive significance of the supernormal pecking response in young Lesser Black-backed Gulls (*Larus fuscus*)

4.1 INTRODUCTION

As discussed in Chapter 3, the pecking response in gull chicks is an innate behaviour, whereby chicks peck at their parents' bills to initiate feeding. The particular features that elicit the pecking response in naïve chicks are the colour and shape of the adult bill and bill markings such as the gonys spot (if present), combined with movement (Tinbergen & Perdeck, 1950; Hailman, 1967; Margolis *et al.*, 1987; Alessandro *et al.*, 1989). Experiments in which these features were separated using various models indicated that heterogeneous summation occurs, such that chicks' responses to each stimulus component add up to give the level of pecking observed towards a complete model containing all components (Margolis *et al.*, 1987; Alessandro *et al.*, 1989). It might be assumed, therefore, that the pecking response of naïve chicks has been optimized through natural selection to respond maximally to such stimuli (Godfray, 1991; Kölliker, 2005), which indicate the presence of an adult, especially given that young rely entirely on their parents for food (Tinbergen, 1953; Spaans, 1971; Bukaciński *et al.*, 1998; Starck & Ricklefs, 1998). However, this is not the case. Rather, chicks peck at a greater rate towards certain stimuli, even if these bear little resemblance to an adult's head (Tinbergen & Perdeck, 1950). The term "supernormal response" has been coined to describe such unusual behaviour, and the stimuli provoking it are thus termed "supernormal stimuli" or "superstimuli" (Tinbergen and Perdeck 1950, Tinbergen 1953).

A supernormal response occurs when an alteration of a natural stimulus results in a more potent response from an animal, whereas the opposite is normally true (Arak & Enquist, 1993; Ghirlanda & Enquist, 2003). Although there are many examples of this phenomenon, the supernormal pecking response in gull chicks is one of the earliest documented, and hence most famous, examples. It was first described by Dutch ethologist Niko Tinbergen and co-workers, following pioneering studies with Herring Gulls (*Larus argentatus*) in the mid-twentieth century (Tinbergen & Perdeck, 1950). Tinbergen's team presented newly hatched chicks with a series of model adult heads, each of which were slightly modified to see how this affected chick behaviour. This led to the discovery that some models, such as those with a long, narrow bill, brought about supernormal pecking responses (Tinbergen & Perdeck, 1950). They also ascertained that the stimulus eliciting the strongest response was quite unlike an adult head. Instead, it was a long, thin, red rod with three white rings near its pointed tip (Tinbergen & Perdeck, 1950) (Fig. 4.1), henceforth referred to as "the superstimulus" (SS).

Fig. 4.1. A Lesser Black-backed Gull (*Larus fuscus*) chick pecking a SS during behavioural tests in June 2007.

4.1.1 Supernormality in the animal kingdom

Animals exposed to a supernormal stimulus show directional (but not necessarily open-ended) preferences (Arak & Enquist, 1993; Ghirlanda & Enquist, 2003), often responding more vigorously to stimuli that are larger, louder, or more colourful than those commonly encountered, as revealed by experimental manipulation. There are many examples of supernormality in nature (see Tinbergen, 1948; Ryan, 1998; Ghirlanda & Enquist, 2003). Studies of incubating birds have shown supernormal responses for particular sizes and colours of egg in several species, including Herring Gulls (Tinbergen, 1951; Baraends & Drent, 1982), Oystercatchers (*Haematopus ostralegus*) (Tinbergen, 1951) Greylag Geese (*Anser anser*) (Tinbergen, 1951) and Pied Flycatchers (*Ficedula hypoleuca*) (Moreno *et al.*, 2008). In the context of mate choice, females respond supernormally to males with experimentally lengthened tails (a sexual ornament) in Widowbirds (*Euplectes progne*) (Andersson, 1982), and female Least Auklets (*Aethia pusilla*) show supernormal preferences for males with crests (as seen in Crested (*A. cristatella*) and Whiskered (*A. pygmaea*) Auklets), despite homospecific males being crestless (Jones & Hunter, 1996). A natural example of supernormality in birds is seen in brood parasites, such as the Common Cuckoo (*Cuculus canorus*), whose chicks are irresistible to their host parents because their large, colourful gapes and intense begging calls are more stimulating than those of the hosts' own chicks (Kilner *et al.*, 1999; Holen *et al.*, 2001; but see Noble *et al.*, 1999).

Non-avian species also exhibit supernormal responses. Many species of fish show supernormal preferences towards red, including Zebrafish (*Danio rerio*) (Spence & Smith, 2008), Three-spined Sticklebacks (*Gasterosteus aculeatus*) and Nine-spined Sticklebacks (*Pungitius pungitius*) (Smith *et al.*, 2004). A well known example from the amphibians is that of female preferences for male mate-attraction calls in Túngara frogs. Males of *Physalaemus pustulosus* have a suffix appended to their mating call. A supernormal preference for this type of ornamentation has been found in females of *P. coloradorum*, even though it does not occur in males of that species, nor in males of the other approximately 40 members of this species group, suggesting that female preference is ancestral to the evolution of the male trait (Ryan & Rand, 1993). In insects, male Silver-washed Fritillary butterflies (*Argynnis paphia*) are stimulated supernormally by an experimentally enhanced frequency of the female wing-flash pattern (Magnus, 1958, cited in Guilford & Dawkins, 1993), while supernormally attractive artificial pheromones can hijack the mechanisms of mate attraction in moths (Jaffe *et al.*, 2007), and females of certain cricket species show supernormal preferences for nuptial gifts, even if this form of mating behaviour has not evolved in that species (Sakaluk, 2000). Humans also show supernormal preferences for the exaggeration of particular physical features (Costa & Corazza, 2006), while it is arguably supernormal responses to particular colours and forms that give works of art their appeal (Ramachandran, 2004).

4.1.2 The evolution of supernormal behaviour

Supernormality appears to result from perceptual biases in an animal, which cause it to respond unusually strongly to particular types of stimuli (Arak & Enquist, 1993; Ryan, 1998), due to properties of that organism's sensory systems or psychology (Spence & Smith, 2008). These "receiver" or "sensory" biases are seen in several animal taxa. They operate in many different behavioural contexts both intra- and interspecifically, and function in several sensory modalities, all suggesting that they are a general feature of animal recognition systems (Arak & Enquist, 1993).

Receiver biases are often divided into two main categories; those that are innate (and thus genetically inherited), and those that are learned (Ghirlanda & Enquist, 2003; ten Cate & Rowe, 2007). Supernormality is usually thought to be the result of hard-wired, innate perceptual biases, such that behavioural responses occur spontaneously with no prior experience of a stimulus (Guilford & Dawkins, 1991; ten Cate & Rowe, 2007). Studies of this subject have traditionally been carried out by ethologists (Ghirlanda & Enquist, 2003). The phenomenon of learned receiver biases, on the other hand, is known as "peak shift", and has typically been a research topic in experimental psychology (Purtle, 1973; Ghirlanda & Enquist, 2003). Peak shift emerges following training of an animal to discriminate between positively rewarded and neutrally or negatively rewarded stimuli that vary along a stimulus dimension (for example, the wavelength of reflected light). An individual's peak behavioural response is then brought about by a novel stimulus that is shifted to a level beyond that of the positive training stimulus, such that it is an exaggerated version of it, and away from the negative stimulus (Hanson, 1959, cited in Rowe & Skelhorn, 2004). This mechanism has been invoked to explain the driving of sexual selection in birds via preferences for exaggerated traits, following sexual imprinting on an individual's parents at the chick stage (ten Cate *et al.*, 2006).

The distinction between supernormality and peak shift is perhaps artificial, with some authors arguing that they are essentially synonymous (Ghirlanda & Enquist, 2003; Jansson & Enquist, 2003). It is perhaps helpful to consider the two as being part of a continuum, differing in their degree of plasticity with respect to prior experience of a stimulus and learning (ten Cate & Rowe, 2007). Both involve the process of generalization, whereby a response to a particular stimulus is expressed in a wider behavioural context, upon encountering a novel stimulus (Purtle, 1973; Ghirlanda & Enquist, 2003). Supernormality and peak shift are also both thought to influence the evolution of signals (Jansson & Enquist, 2005; Lynn *et al.*, 2005; ten Cate & Rowe, 2007), although peak shift can only do so through modification of existing traits, whereas supernormality can explain the innovation of novel characteristics too (Rowe & Skelhorn, 2004).

Two main explanations are usually cited for the evolution of innate receiver biases. The first is that they are an incidental byproduct of natural selection on a particular sensory system (Arak & Enquist, 1993; Endler & Basolo, 1998; Ryan, 1998; Ramachandran, 2004). It is therefore possible that a species will react strongly to a novel stimulus that happens by chance to excite an individual's sensory system in a way never experienced during the adaptation to the relatively small number of stimuli encountered during the species' evolutionary history. Until an animal is exposed to this type of stimulus, such perceptual preferences remain hidden (Arak & Enquist, 1993). Various simple neural network models have been used to demonstrate that receiver biases can drive the evolution of stimuli such that they assume supernormal properties for no adaptive reason. This is because of directional preferences for supernormality in the individuals responding to a stimulus, eliciting asymmetrical selection pressures on the type of stimulus chosen (Arak & Enquist, 1993; Enquist & Arak, 1993). Models examining the preferences of chickens (*Gallus gallus domesticus*) have demonstrated similar findings (Jansson & Enquist, 2003; 2005).

The second explanation of innate receiver biases is that they could arise through the co-option of sensory or psychological processes that are already adapted for another function (Endler & Basolo, 1998; Ryan, 1998; Rowe & Skelhorn, 2004; ten Cate & Rowe, 2007). Examples of this are the innate preferences for red mates in females of various fish species (whether or not males are red in nature), as this colour is important in a foraging context, indicating the presence of particular foodstuffs, or contained nutrients, namely carotenoids (Rodd *et al.*, 2002; Smith *et al.*, 2004, Spence & Smith, 2008).

Whatever the reason underlying the evolution of innate receiver biases, they can drive the evolution of animal signals in ways that may give a selective advantage to both the signaller and receiver. For example, male bowerbirds construct large, elaborate bowers to attract mates. These bowers are often decorated with objects of the same colour as items commonly found in these birds' diets, indicating a pleiotropic effect of foraging preferences becoming selected for as a sexual ornament through female receiver bias (Madden & Tanner, 2003; but see Borgia & Keagy, 2006). However, once this selection comes into play, males building especially attractive bowers gain the advantage of finding a mate, and females may be able to assess aspects of potential males' genetic fitness through the quality of bowers produced, leading to "good genes" sexual selection mediated by the Handicap Principle (Zahavi, 1975), or unfakeable indices of male quality (Maynard Smith & Harper, 2003). Similar principles could drive the evolution of supernormal stimuli as part of effective signalling systems in other behavioural circumstances.

4.1.3 Supernormality in the pecking response

The supernormal response that Tinbergen and Perdeck (1950) discovered in gull chicks could therefore be the result of non-adaptive, hidden preferences due to incidental aspects of these birds' nervous systems, or an adaptation of pre-existing preferences from a different behavioural context. Tinbergen and Perdeck's (1950) own view was somewhat different to either of these possibilities. They suggested that the supernormal response had an adaptive significance as an artefact of the ventro-lateral view by which hatchlings may often perceive their parents' gonys spots for the first time (Tinbergen & Perdeck, 1950). From beneath, the red gonys appears elongated compared to the side view (Fig. 4.2), so since chicks are genetically predisposed to aim their pecks at this area, they may possess supernormal preferences for exaggerated versions of such a feature (Tinbergen & Perdeck, 1950). However, this explanation does not account for why the white stripes of the SS are attractive,[29] nor why chicks from species without a gonys spot, such as Black-headed Gulls (*Chroicocephalus ridibundus*) (Weidmann & Weidmann, 1958), Laughing Gulls (*Leucophaeus atricilla*) (Hailman, 1967) and Ring-billed Gulls (*L. delawarensis*) (Conover & Miller, 1981), also show supernormality in the pecking response, suggesting that this behaviour is governed by features of a chick's sensory perception that predate the evolution of the gonys spot, an innovation that probably only occurred once during the relatively recent radiation of species in large white-headed gull species group (Pons *et al.*, 2005; Ferns and Ross-Smith, 2009). It is also not certain that chicks would generally view their parents' bills from below,

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[29] The authors stated that the white stripes were an effective stimulus because they added contrast (Tinbergen & Perdeck, 1950).

especially given that they are semi-precocial, and move around the nest soon after hatching.

Fig. 4.2. Adult Lesser Black-backed Gull bill viewed (a) from the side (b) from underneath. This individual has an unusually large gonys spot, with a substantial area of red on the upper mandible, and a prominent orbital ring.

Another viewpoint is that the chick pecking response simply reflects the colour of the adult beak (Cullen, 1962). Chicks of several larid species have and innate preference for red. Some, such as the Black-legged Kittiwake (*Rissa tridactyla*), which do not have an area of red on the bill, do however have a red throat, and it is from this region that parents feed their chicks (Cullen, 1957; Cullen, 1962), while Sandwich Tern (*Sterna sandvicensis*) chicks, (whose parents have black beaks with yellow tips and gapes), have an innate preference for black (Weidmann, personal communication, cited in Cullen, 1962). It is therefore possible that the supernormal response reflects a preference for objects sharing the colour of the bill. However, this argument is somewhat circular, as there is no way of testing if chick preference adapted to adult bill colour or vice versa (Cullen, 1962). It also does not provide an explanation for the role of the white stripes or the thin shape in the supernormal response.

If the supernormal pecking response is simply a byproduct of the chicks' sensory systems, it could still drive the evolution of bill colouration towards containing some of the features of the SS. As gull chicks rely completely on their parents for food, any evolutionary innovation that would facilitate this process would increase the likelihood of offspring survival and help to optimize parental lifetime success. This could lead to characteristics such as a red spot or coloured bill tip, becoming fixed in the population. An indication that gull chicks might have an ancestral sensory bias for features such as the red gonys spot was found in a study of Laughing Gulls, which is a species in which adults do not have bill markings, whose chicks aimed pecks at the bill tips of models of Laughing Gull and Ring-billed Gull adults, but at both the gonys spot and the bill tips of model American Herring Gulls (*L. smithsonianus*) (Hailman, 1962).

Assuming the supernormal response is not merely an "accidental feature" of the chick's nervous system (Ramachandran, 2004), it might have arisen through generalization from other functions, for example foraging or sexual signalling. Measurements of the bill at the gonys spot and elsewhere, show spectral reflectance typical of colours mediated by carotenoids (Fig. 4.3), which are frequently important in both these behavioural contexts.

Carotenoids are essential to the health of many animals, enhancing both cell-mediated and humoural immunity, as well as acting as antioxidants, which are thought to help to prevent cancer, cardiovascular diseases and neurodegeneration (Chew, 1996; Chew & Park, 2004). However, carotenoids cannot be synthesized *de novo* by animals, and must hence be obtained through the diet (Goodwin, 1984, cited in McGraw *et al.*, 2002). Thus, the nutritional need for carotenoids, which are often orange or red, may help explain the evolution of hard-wired preferences for these colours in so many species.

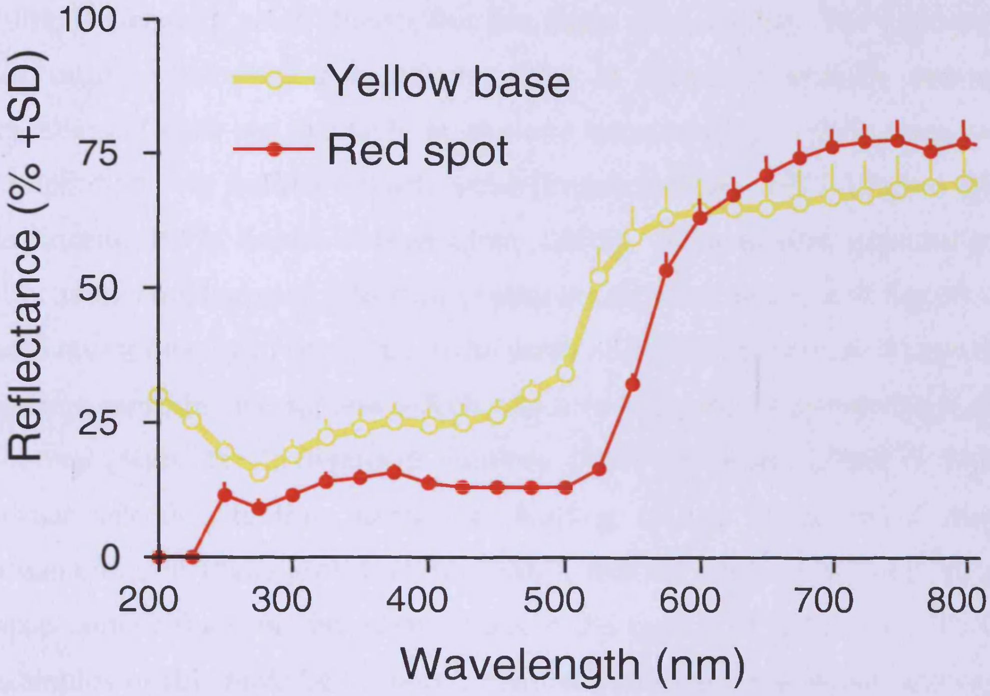

Fig. 4.3. The spectral reflectance of the bill of a dead adult *L. fuscus*. Compare to Fig. 3.4 to see the difference between bill reflectance of dead and living gulls.

As described in section 4.1.2, such innate receiver biases for colours associated with food items, appear to have driven the evolution of sexually selected red colouring in several species, ranging from birds to fish (Badyaev & Hill, 2000; Rodd *et al.*, 2002; Blount *et al.*, 2003; Smith *et al.*, 2004; Spence & Smith, 2008). One of the reasons that carotenoids can be used as sexual signals is that their expression provides a reliable indicator of genetic and phenotypic fitness. This is because only individuals that are disease free (indicating a healthy immune system for resisting pathogens), and find sufficient time and energy to foraging, can exhibit intense carotenoid colouration (McGraw & Hill, 2000; Peters *et al.*, 2004).

Gulls (and other larids) are socially monogamous, often pairing with the same partner for their entire reproductive lives (Tinbergen, 1953; Coulson, 1966; Annett & Pierotti, 1999). Additionally, very low levels of extra-pair paternity and egg-dumping by foreign females have been reported (Conover, 1984;

Mills, 1994; Bukacińska *et al.*, 1998; Gilbert *et al.*, 1998; González-Solís *et al.*, 2001; Helfenstein *et al.*, 2004b, but see Duda *et al.*, 2008). The operational sex ratio is therefore approximately 1:1 in terms of sexually receptive members of each sex available at any one time, leading to little intrasexual competition over mating opportunities (Emlen & Oring, 1977; Clutton-Brock & Vincent, 1991; Kokko & Monaghan, 2001). Such mating systems exert effectively equal sexual selection pressures on both males and females, as both invest heavily in courtship, incubation and parental care, and have their lifetime reproductive success affected to a very similar extent through chick survival (Mills, 1994; Owens & Bennett, 1997; Cockburn, 2006).[30] Mutual sexual selection is thus predicted, leading to the evolution of mutual ornamentation (Kraaijeveld *et al.*, 2007), that is, ornaments seen in both sexes convey the same information about the quality of the bearer. Various examples of this have been found, including amongst the larids, where the sexually monomorphic moustache feathers and wattles of Inca Terns (*Larosterna inca*) are a reliable indicator of parental condition, reproductive output and chick fitness (Velando *et al.*, 2001).

The gonys spot could be another example of a mutual ornament, functioning as a carotenoid-mediated signal of quality in both sexes. Evidence that it does honestly reflect quality comes from the finding that dietary carotenoid supplementation of breeding female Lesser Black-backed Gulls intensifies not only integument colouration, but also egg quality, with profound fitness implications for offspring (Blount *et al.*, 2002), while in female Great Black-backed Gulls (*L. marinus*), gonys spot colour intensity was positively related to egg and clutch size, as well as to circulating lymphocyte levels (Kristiansen *et al.*, 2006). In males, dietary supplementation increased gonys spot size and circulating plasma carotenoid levels in Yellow-legged Gulls (*L.*

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[30] Although intrasexual competition is low, intersexual competition occurs, with females trading copulations to gain courtship feedings (González-Solís *et al.*, 2001; Velando, 2004; Kempenaers *et al.*, 2006) and through this process assessing male quality for long-term pairing (Tasker & Mills, 1981; Helfenstein *et al.*, 2003b) and ejecting sperm if quality is poor (Helfenstein *et al.*, 2003a).

michahellis) (Pérez *et al.*, 2008), and spot colour intensity has been shown to reflect body condition of Great Black-backed Gulls (Kristiansen *et al.*, 2006), again indicating an honest mechanism for signalling quality.

Such integument-based ornaments are dynamic, in that they change according an individual's condition, allowing their partner to continuously assess their quality at any given moment and adjust their behaviour accordingly (Kraaijeveld *et al.*, 2007). This has been cited as the reason that mutual ornaments are frequently displayed both before and after pair formation, such that individuals can attune their parental investment to that which their partner is capable of providing at the time (Kraaijeveld *et al.*, 2007). Indeed, Yellow-legged Gulls have been shown to adjust their parental effort in response to experimental manipulation of their partner's gonys spot size, which is turn affected the amount of parental care the manipulated bird was required to perform (Morales *et al.*, 2009).[31]

Supernormal preferences in gull chicks could thus be tapping into a sexually selected preference for particular colours, which has in turn been generalized from foraging adaptations. However, this hypothesis does not explain why features of the SS other than its colour are attractive. An alternative idea is that the SS is effective because it reflects innate foraging preferences, with the possibility that the particular foodstuffs favoured are those required by chicks in early life.

As adults, gulls consume a wide variety of food substances, from small invertebrates and fish to human refuse (e.g. Harris, 1965; Threlfall, 1968; Hunt & Hunt, 1973b; Mudge & Ferns, 1982). However, when feeding their chicks, particularly during the first week post-hatching, adults adapt their foraging patterns to increase the proportion of soft-bodied food consumed,

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[31] The melanin-mediated black bill tips found in some other larids might serve a similar signalling function to the red spot in large white-headed gulls. The size and intensity of the black area, at which begging chicks peck, has been found to honestly reflect phenotypic quality in Arctic Terns *(S paradisaea)* (Møller *et al.*, 2007).

especially worms and small fish (e.g. Annett & Pierotti, 1989; Pedrocchi *et al.*, 1996; Stanworth, 1998). Such dietary switches are thought to address the young's nutritional needs and/or ability to physically manipulate food items (Kirkham & Morris, 1979; Annett & Pierotti, 1989; Nogales *et al.*, 1995; Stanworth, 1998). The diets of adults and chicks are discussed in detail in Chapter 5.

If the dietary differences between gulls during the early chick phase and adulthood are governed by the specific demands of young chicks, this could have led to selection pressure on chicks' innate feeding preferences, so that they are adapted to peck at objects resembling the food items they require from hatching. Such selection pressure could be intensified by sibling competition for food, as parents do not tend to feed chicks individually (Henderson, 1975; Mathevon & Charrier, 2004; but see Burger & Gochfeld, 1996), and it would pay to peck immediately at the optimum food substances, particularly for chicks lower in the brood hierarchy. Worms, insect larvae and small fish may be elongated, reddish in colour and have rings or stripes along their length, not unlike the SS. Indirect evidence that the supernormal pecking response may tap into chicks' dietary preferences comes from the finding that chicks produced peeping calls when presented with models resembling real heads, but were relatively silent with rod models such as the SS, even though they pecked at them vigorously (Conover & Miller, 1981). The authors of this research concluded that chicks vocalized when near their parents, so the fact that they did not emit vocalizations with SS models suggests that these chicks perceived them as food, and not a parent's bill (Conover & Miller, 1981).

4.1.4 Factors influencing the supernormal response

As detailed in section 3.1.2.2 several possible factors, including chick age and laying order, could shape the pecking response. It was thought that these might also affect the nature of the supernormal response, and hence attempts were made to account for these factors in the experiments carried out.

4.2 EXPERIMENTAL QUESTIONS

The experiments detailed in this chapter set out to explore the following questions about the supernormal pecking response:

1) Was Tinbergen correct in his hypothesis that the SS is effective at stimulating chick pecking because it resembles the underside of an adult's bill?[32]
2) What is the role of each distinguishing feature of the SS (i.e. its length, width, red colour and stripes) in evoking the supernormal response?
3) Is the supernormal pecking response influenced by other factors, such as egg laying order, chick age or the type of stimuli encountered by a chick in early life?

4.3 METHODS

Fieldwork was carried out with Lesser Black-backed Gulls on Flat Holm in three consecutive breeding seasons, from 2006 to 2008. Methods of chick selection and care are described in sections 2.3.1 and 2.3.2. The basic protocol for behavioural experiments was identical to that detailed in section 3.3.2.1. All work was carried out under licence numbers OTH:SB:02:2006/2007/2008 from the Countryside Council for Wales, and conformed to the guidelines on the ethical treatment of animals in behavioural research, set by the Association for the Study of Animal Behaviour.

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[32] Despite the acclaim that Tinbergen and co-workers received for the discovery of the supernormal response in gull chicks, little subsequent work has concentrated on the mechanism governing it. Recent publications have revisited other aspects of this study (ten Cate 2009; ten Cate *et al.*, 2009; Morales *et al.*, 2009), but it appears that nobody has tested Tinbergen and Perdeck's (1950) own hypothesis that the SS taps into an innate chick preference for long, thin objects, reflecting the angle at which a newly hatched individual crouching in the nest beneath its parent would first view its bill, with the entire beak seeming narrow, and the gonys spot appearing as an elongated, thin, red mark.

Experiment 4.1 - Testing Tinbergen and Perdeck's explanation of the supernormal pecking response

This experiment was designed to test Tinbergen and Perdeck's (1950) hypothesis about the mechanisms governing the supernormal pecking response. The experiment was carried out with 31 naïve (incubator-hatched) chicks on four dates between 21st May and 8th June 2008. Mean age at the start of experimentation was 23.3 hours, with a range of 3.8 to 40.8 hours. Chicks' reactions to three different stimuli were tested (Fig. 4.4). The Control was a two-dimensional stick-mounted card model of an adult Lesser Black-backed Gull head in profile (gonys spot diameter = 10.0 mm, bill length = 53.0 mm, bill depth at gonys = 16.5 mm). This was compared with a 3 mm diameter SS (stripe width = 2 mm, distance between stripes = 2 mm, distance from tip to first stripe = 16 mm), and a two-dimensional stick-mounted card model of the ventral underside of an adult Lesser Black-backed Gull head (Ventral) (gonys spot = 3 mm wide x 15 mm long, bill length from tip to end of gape = 66 mm). The Control and SS were modelled on photographs and drawings of those used by Tinbergen and Perdeck (Tinbergen & Perdeck, 1950; Tinbergen, 1953), with features of the Control, such as the eye, modified to appear more realistic. The dimensions of the Control were designed to be within the range found in the wild (Malling Olsen & Larsson, 2004), while those of the SS were optimized through experiments 4.2a and 4.2b. The remaining Ventral stimulus was based on Tinbergen and Perdeck's (1950) drawing of the underside of the adult head, and photographs of adult Lesser Black-backed Gulls from beneath. Its size was scaled to match that of the Control. To minimize pseudoreplication of stimuli (Kroodsma, 1990; Ruxton & Colegrave, 2006), six different replicates of each stimulus were available (three right hand views and three left hand views in the case of the Control), and the choice of replicate selected at random for each trial by rolling a die. The order of stimulus presentation to each chick was randomized in the same fashion.[33]

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[33] Randomization was without replacement, such that no chick was presented with the same model twice.

Fig. 4.4. Examples of the three stimuli used in experiment 4.1. Left to right: SS, Ventral, Control.

Experiment 4.2 - The role of individual superstimulus features in the supernormal response

4.2a Determining the optimum diameter of the superstimulus

Experiments were conducted using SS of diameters 1 mm, 2 mm, 3 mm, 4.5 mm, 6 mm, 10 mm, 12 mm, according to which stripe width and separating distance were also scaled. The SS were made from painted knitting needles, the colour of which is shown in Fig. 4.5. The experiment was carried out on 54 chicks on five dates between 22nd May and 11th June 2006. Chicks were of unknown age and experience at the time of testing, as they were removed from the parental nest post-hatching. On each day of testing, half the chicks were given the stimuli in order of ascending diameter, and the other half in descending order.

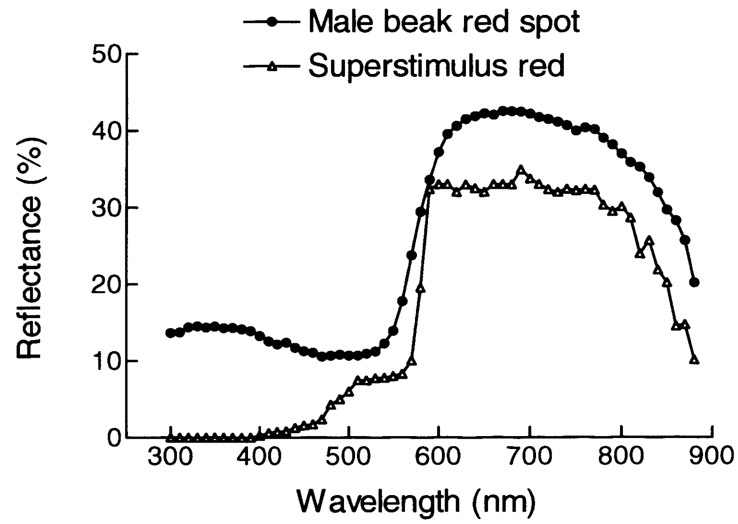

Fig. 4.5. The spectral reflectance of the red paint used for the SS, compared to the red gonys spot of a breeding male Lesser Black-backed Gull. The percentage reflectance of the SS is low because this was a 3 mm diameter SS with pronounced curvature to its surface (the same red paint was used for SS of all diameters). It was thus difficult to measure.

4.2b Assessing the effect of superstimulus stripe number and width

Chicks in each trial were given a choice between two different two-dimensional stretches of card of equal length and thickness (9 cm long by 5 mm wide) running in parallel and separated by 20 mm. At one end, the lengths of card ("arms") were joined to a piece of white card, such that both formed part of the same stimulus object (e.g. Fig. 4.6). The background colour of each arm matched the shade of red used for the gonys spot on the card models described in experiment 4.1 (Fig. 3.4a)

4.2bi Choice of three stripes or no stripes

These experiments were designed to investigate whether the SS does indeed provoke a stronger pecking response than a red rod without stripes. Four different stimuli were used. For each stimulus, one arm had three white stripes, while the other was uniformly red. On the striped arm, stripe thickness varied between stimuli. Chicks were therefore given a choice of a red arm against one with 1 mm, 2 mm, 3 mm or 6 mm stripes. The position of the two arms (left or right) was randomly determined for each stimulus. Ten different chicks of unknown age and experience (i.e. taken from the parental nest post-hatching) were tested on 10th June 2006. Half the chicks were presented with the stimuli in order of ascending stripe thickness, while the other half was tested in reverse order.

4.2bii Choice of multiple stripes or no stripes

These behavioural trials aimed to elucidate whether a red rod with stripes along its length would bring about a different response to a plain red rod. Four different stimuli were used. For each stimulus, one arm had white stripes of set thickness all the way along its length, while the other was uniformly red. On the striped arm, stripe thickness varied between stimuli. Chicks were therefore given a choice of a red arm against one with 1 mm, 2 mm, 3 mm or 6 mm stripes. The position of the two arms was again randomly determined. Ten different chicks of unknown age and experience (removed from the nest after hatching) were tested on 10th June 2006, with half presented the stimuli in order of ascending stripe thickness, and the other half in reverse order.

4.2biii Choice of three stripes of different widths

These trials were conducted to determine if stripe width affected the supernormal pecking response, with a view to ascertaining the optimum thickness. Three different stimuli were used. Each had three white stripes positioned towards the terminal ends of its arms, such that the first was 9 mm from the end. The thickness of these stripes was different on each arm, to give chicks a choice between 1 mm or 2 mm, 2 mm or 3 mm, and 3 mm or 6 mm stripes. Whether the arm with thicker stripes was to the left or the right of the one with thinner stripes was randomly determined. 45 chicks of unknown age and experience (collected from the colony post-hatching) were used on six separate days between 21st May and 14th June 2006. On each day, half the chicks were presented with the stimuli in the order 1 mm v 2 mm, 2 mm v 3 mm, 3 mm v 6 mm, and the other half in reverse order.

4.2biv Choice of multiple stripes of different widths

These trials aimed to determine if the supernormal pecking response to a stimulus with multiple stripes could be altered by using stripes of different thicknesses. Four different stimuli were used. Each had white stripes placed at regular intervals along the length of the arms, starting with a stripe 9 mm from the arm's end. The thickness of these stripes varied between the two arms, such that the chicks were given a choice of 1 mm or 2 mm, 1 mm against 3 mm, 2 mm or 3 mm, and 3 mm or 6 mm. The orientation (left or right) of the two arms was randomly determined. The experiments were carried out with 35 different chicks of unknown age and experience (taken from the nest after hatching) on four separate dates between 31st May and 13thJune 2006. On each day, half the chicks were presented with the stimuli in the order 1 mm v 2 mm, 1 mm v 3 mm, 2 mm v 3 mm, 3 mm v 6 mm, and the other half in reverse order.

4.2bv Choice of three stripes or multiple stripes

This experiment was designed to test whether an SS (with three terminal stripes) is more or less appealing to chicks than a stimulus with stripes all along its length. Four different stimuli were used. For each, one arm had only three white stripes, while the other had white stripes along its whole length (Fig. 4.6). The width of these stripes was the same for each of the two arms. Chicks were given a choice of arms for stripes of 1 mm, 2 mm, 3 mm and 6 mm thicknesses. Random allocation was used to decide which arm should be to the left or the right. Tests were run with 46 chicks of unknown age and experience (removed from their parents post-hatching) on five separate dates between 26th May and 14th June 2006. On each day, half the chicks were presented with the stimuli in order of ascending stripe thickness, while the other half was tested in reverse order.

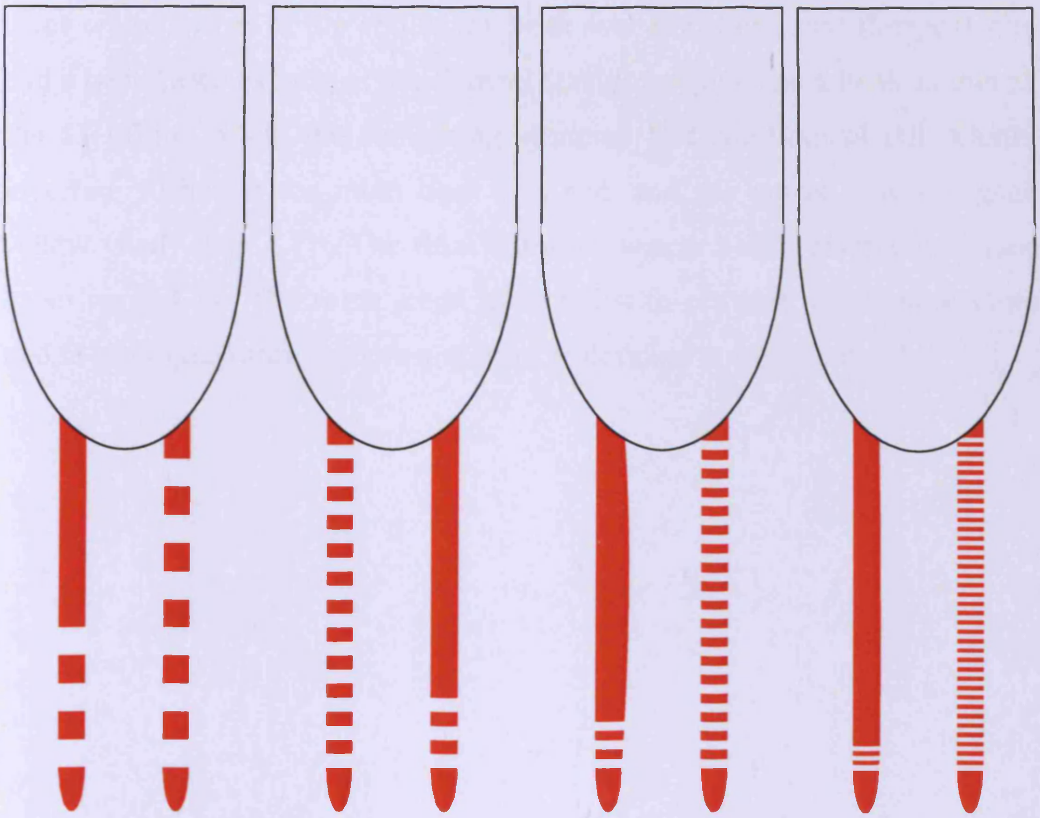

Fig. 4.6. The choice of stimuli presented in experiment 4.2bv. Stimuli in all other parts of Experiment 4.2b were similar apart from adjustments to the arms, as described in the text.

4.2c Isolating the effect of individual features of the superstimulus

The individual features of the SS that could be responsible for the supernormal pecking response are its extended length, red colour, thinness and the three white stripes (Tinbergen & Perdeck, 1950). This experiment was designed to quantify the effects of each of these characteristics individually, by comparing a control model and an SS with model heads modified by adding each feature in turn.

This experiment was carried out on 22 naïve (incubator-hatched) chicks on three dates between 26th and 29th May 2008. All chicks were between 13.5 and 42.5 hours old at the time the experiment commenced, with a mean age of 27.2 hours. Chicks' reactions to six different stimuli were tested. The Control was the same as that described in experiment 4.1. Four of the five other stimuli were identical to the control in all except one feature, which was altered to add one characteristic of the SS. Thus, one stimulus type had three white stripes at the end of the beak over the gonys spot (Stripes), one had a beak twice as long as the Control (Long) and one had a beak as thin as the SS (Thin), while the remaining stimulus had the Control bill colours inverted, such that the main beak was red, and the gonys spot and gape yellow (Red) (Fig. 4.7). The final stimulus was a 3 mm diameter SS (see experiment 4.1). The same steps were taken to prevent pseudoreplication and to randomize stimulus presentation as detailed in experiment 4.1.

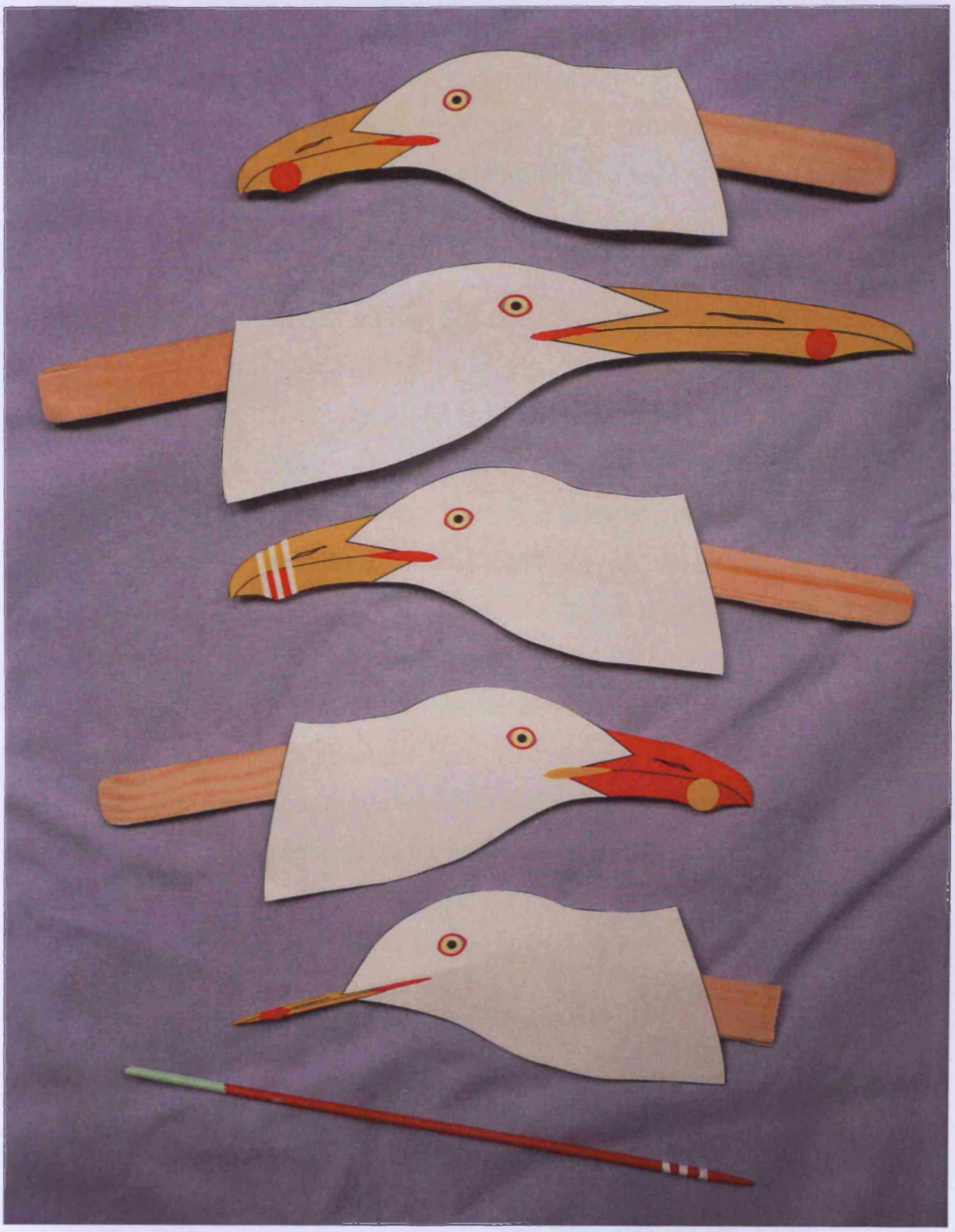

Fig. 4.7. Examples of the stimuli used in experiment 4.2c. Top to bottom: Control, Long, Stripes, Red, Thin, SS.

4.2d Deleting individual features of the superstimulus

This experiment was similar to experiment 4.2c, except that tests were carried out to quantify the relative importance of the characteristics of the SS by the elimination of a single factor at a time, using a Control model beak plus three of the four SS features (length, thinness, red colour and stripes).

The experiment was carried out on 22 naïve (incubator-hatched) chicks on 1st and 4th June 2008, with 8 and 14 chicks respectively. All chicks were between 7.5 and 41.5 hours old at the time the experiment commenced, with a mean age of 25.9 hours. Chicks' reactions to six different stimuli were tested. The Control was the same as that used in experiment 4.1. Four of the five other stimuli were based on the Control with the addition of three characteristics of the SS (Fig. 4.8). Thus, one stimulus type had a beak that was the width of the SS, twice the length of the Control and with the bill colouration reversed such that the main beak was red and the gonys spot and gape were yellow. This stimulus type was termed LTR (long, thin, red). Another stimulus was long and thin with three white stripes over the gonys spot, termed LTS (long, thin, stripes), while the remaining combinations were a long, red and striped stimulus (LRS), and a thin, red and striped stimulus (TRS). The chicks were also presented with a 3 mm diameter SS. As in experiment 4.1, the models were based on those used by Tinbergen and Perdeck (1950), stimulus order was randomised and precautions were taken to avoid pseudoreplication.

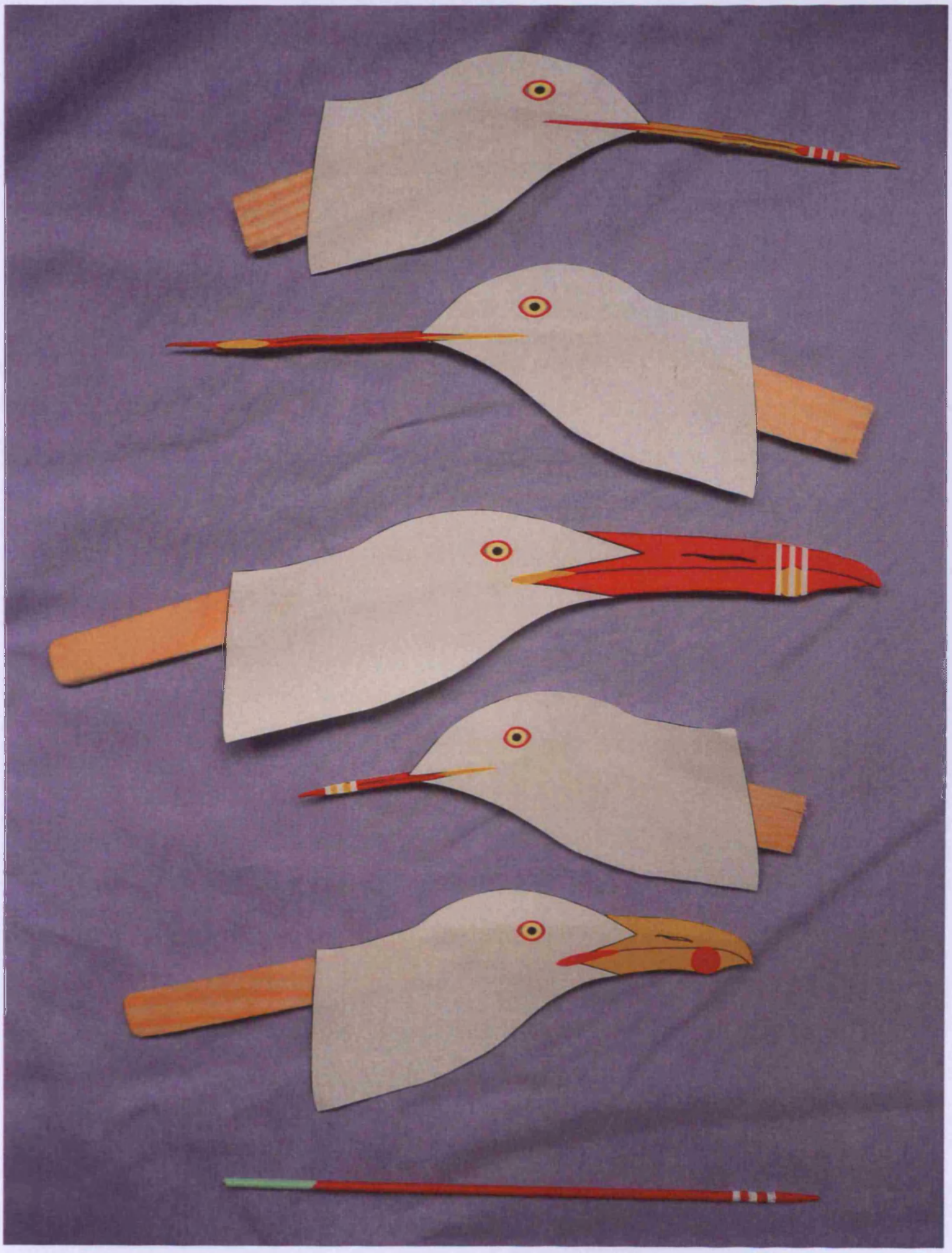

Fig. 4.8. Examples of the stimuli used in experiment 4.2d. Top to bottom: LTS, LTR, LRS, TRS, Control, SS.

Experiment 4.3 - External and intrinsic effects on the supernormal pecking response

4.3a Effect of extrinsic factors on supernormal pecking

In 2007, the effects of laying order, chick age, sex, egg volume, experimental date and nearest neighbour distance on supernormal pecking were evaluated by taking naïve (incubator-hatched) chicks and exposing them to one of sixty randomly selected replicates of a 3 mm diameter SS (for methods of molecular sexing, see Appendix II). This was used as the standard stimulus as it was thought to elicit the maximum motivation to peck. This experiment was carried out on 52 chicks on nine separate dates between 24th May and 13th June 2007. The youngest chick was 14 hours old and the oldest 48 hours, with a mean age of 34.2 hours.

4.3b Supernormal pecking and stimulus experience

In 2008, an SS was used in every set of experiments carried out, such that the possible effect of the other stimuli used during the experiment on the supernormal pecking response could be assessed. The pecking responses to the SS were thus extracted for 85 chicks taking part in experiments 4.1, 4.2c, 4.2d and experiment 5.2 (looking at the addition of "food" items at the end of the bill tips).[34] These took place on 13 separate dates between 21st May and 14th June, with naïve (incubator-hatched) chicks aged between 3.8 and 48.3 hours old (mean age was 26.1 hours post-hatching).

4.3.1 Statistical treatment

Analyses were carried out with Resampling Statistics 3.0.7 (Resampling Stats Inc., 1995) and R version 2.8.1 (R Core Development Team, 2008). Graphical figures were prepared in R version 2.8.1 (R Core Development Team, 2008) and GraphPad Prism 2.01 (GraphPad Software Inc., 1996).

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[34] The experiment on scrambling beak features (experiment 3.4) was excluded from these analyses as the sample size (nine chicks) was much smaller than for the other sets (between 22 and 31 chicks).

Resampling (Simon, 1995) was used to assess the preferences of individual chicks for the choice of arms in experiment 4.2b. The number of pecks each chick actually made to each arm was allotted randomly, and the total number of randomly allocated pecks by all individuals to the arms was tallied. This procedure was repeated 10,000 times and the proportion of totals as large as, or larger than, that actually given to the preferred arm was calculated. The results were divided into three categories based on the levels of pecking performed by each chick. This was done to ensure that individuals with a different level of motivation to peck, and/or ability to do so, were not confounded with each other. In other analyses, this was achieved by including the potentially confounding factors (e.g. chick age and laying order) as explanatory variables in the relevant models, in a process which is not possible with resampling.

Many of the models used to analyse experiments 4.1, 4.2c, 4.2d, 4.3a and 4.3b were similar to those in section 3.3.3, in that the same explanatory variables were included, and model simplification proceeded by the same method. Linear mixed-effects models (LMMs) (Pinheiro & Bates, 2000) were fitted in the "nlme" R package (Pinheiro *et al.*, 2008) to assess the total number of pecks to each model per trial in all these experiments except 4.3b and 4.3c, where a general linear model sufficed (Grafen & Hails, 2002), as each chick only corresponded to one data point in the model. A generalized linear mixed model (GLMM) (Bolker *et al.*, 2009) with a Poisson error was fitted in the "lme4" R package (Bates *et al.*, 2008) for experiment 4.2a. In all mixed models, chick identity was included as a random factor. *Post-hoc* comparisons of the different levels of statistically significant categorical explanatory variables were carried out in the "multcomp" package (Hothorn *et al.*, 2008). GLMMs with a binomial error were employed to examine the proportion of pecks each chick aimed at either the gonys spot or elsewhere for all models (except the SS) in experiments 4.2c and 4.2d, with chick identity again fitted as a random factor. This was again undertaken in the "lme4" package. Statistical tests were two-tailed, with the significance level set at 0.05 and values are presented as the arithmetic mean ± S.E.

4.4 RESULTS

Experiment 4.1 - Testing Tinbergen and Perdeck's explanation of the supernormal pecking response

Only three explanatory variables were found to have a significant effect on chick pecking. The first of these was the stimulus type (LMM, $F_{2,56} = 20.00$, $p < 0.0001$). At 21.74 ± 1.09 pecks per 30 seconds, the SS elicited significantly more pecks than either the Control (17.13 ± 1.16) or the Ventral (16.23 ± 0.92) models (Fig. 4.9), which did not vary significantly from each other in their effect (Table 4.1). The rate of pecking increased significantly with chick age (LMM, $F_{1,29} = 9.55$, $p = 0.0044$). Age also interacted significantly with stimulus type (LMM, $F_{2,56} = 5.26$, $p = 0.0081$), with the relationship between chick age and chick pecking rate increasing more steeply for the SS than for the Control and Ventral stimuli, and Ventral having the shallowest slope of all. Order of stimulus presentation was also significant (LMM, $F_{2,56} = 3.58$, $p = 0.0345$), such that if a stimulus was the third presented, it elicited significantly fewer pecks than the first presented stimulus (LMM, $t_{56} = -2.89$, $p = 0.0054$). There were nonsignificant decreases in pecking rate between the first and second, and the second and third, stimulus presentations.

A significantly higher proportion of pecks was directed at features other than the gonys spot for the Control (19.4%) than for the Ventral (10.9%) stimulus (GLMM, $z = 4.08$, $p < 0.0001$). The largest proportion of these "stray" pecks was aimed at the model's eye for the Control (63.1%), and at the gape for the Ventral stimulus (34.5%).

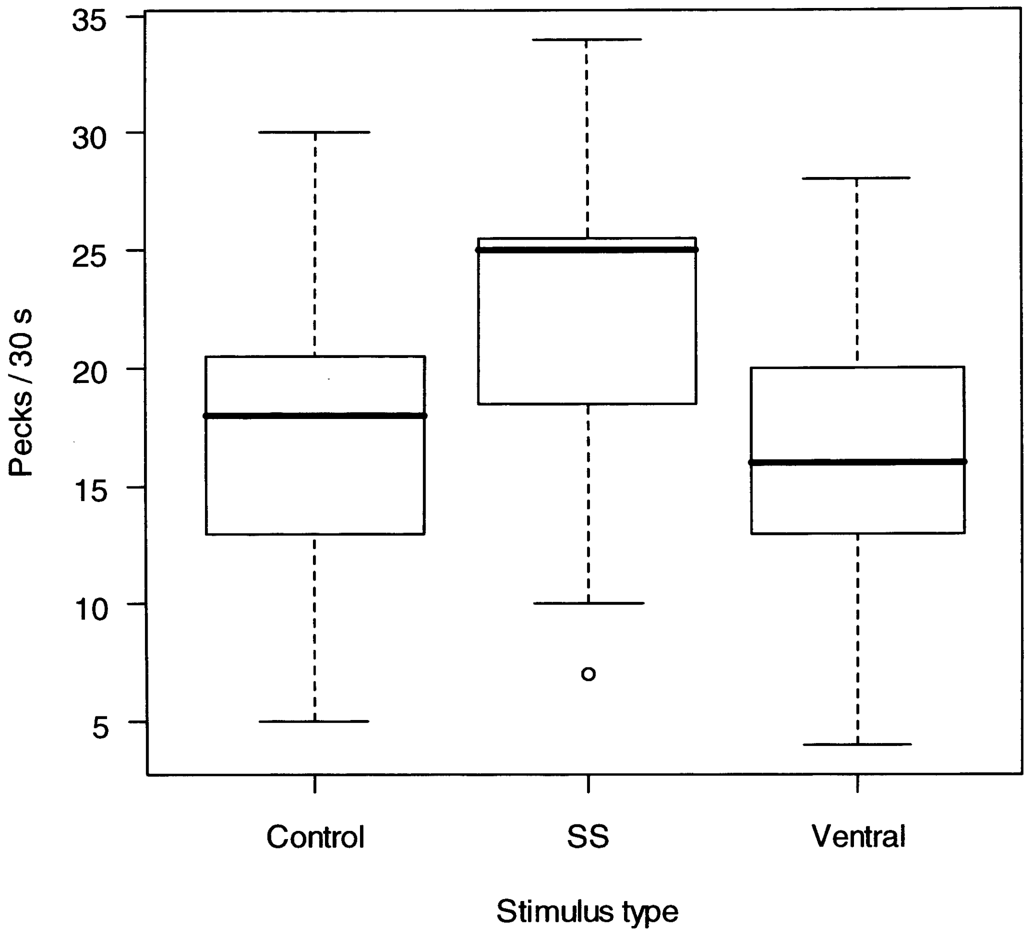

Fig. 4.9. Effect of stimulus type on chicks' pecking response: the SS elicited a greater rate of pecking than either the Control or Ventral stimuli.

Comparison	Estimate*	z	*p*
SS-Control	4.61	4.43	**<0.0001**
Ventral-Control	-0.90	-0.87	0.6610
Ventral-SS	-5.52	-5.30	**<0.0001**

Table 4.1. Pairwise comparisons of least squares means estimates for chick pecking response to different models, with *p*-values adjusted for multiple comparisons. * S.E. = 1.04. Significant values in bold.

Experiment 4.2 - The role of individual superstimulus features in the supernormal response

4.2a Determining the optimum diameter of the superstimulus

SS diameter was the only factor in the fitted models that significantly predicted pecking rate (GLMM, $z \geq 31.81$, $p < 0.0001$) (Fig. 4.10). There was no significant effect of chick mass, presentation order or experimental date.

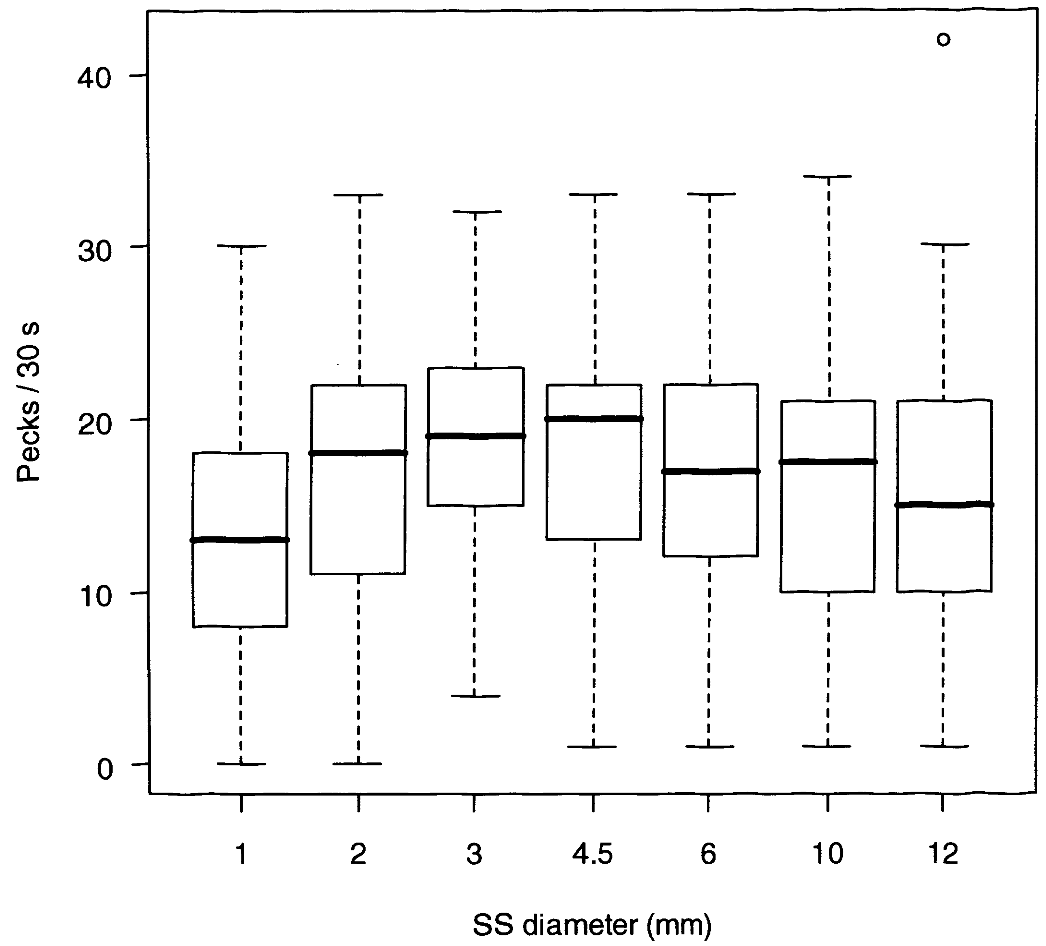

Fig. 4.10. The relationship between SS stimulus diameter and chick pecking rate in experiment 4.2a. Optimum SS diameter for eliciting the supernormal response is approximately 3 - 4.5 mm.

Post-hoc multiple comparisons showed that all diameters were significantly more attractive than the 1 mm SS (13.30 ± 1.08 pecks per 30 seconds), while the 4.5 mm SS (18.60 ± 1.05 pecks) also elicited significantly more pecks than either the 10 mm (16.13 ± 1.11 pecks) or the 12 mm (15.66 ± 1.12 pecks) diameter stimuli (Table 4.2). The stimulus that had the highest mean rate of pecking was the 3 mm stimulus at 18.61 ± 1.03.

Comparison	Estimate*	z	*p*
2 – 1	0.26	5.27	**< 0.0001**
3 – 1	0.30	5.77	**< 0.0001**
4.5 – 1	0.34	6.80	**< 0.0001**
6 – 1	0.24	4.67	**< 0.0001**
10 – 1	0.19	3.62	**0.0050**
12 – 1	0.16	3.18	**0.0240**
3 – 2	0.04	0.81	0.9840
4.5 – 2	0.07	1.56	0.7090
6 – 2	-0.03	-0.61	0.9960
10 – 2	-0.08	-1.65	0.6470
12 – 2	-0.10	-2.11	0.3490
4.5 – 3	0.03	0.64	0.9950
6 – 3	-0.07	-1.38	0.8110
10 – 3	-0.12	-2.36	0.2160
12 – 3	-0.14	-2.79	0.0780
6 - 4.5	-0.10	-2.17	0.3125
10 – 4.5	-0.15	-3.20	**0.0230**
12 – 4.5	-0.17	-3.66	**0.0050**
10 – 6	-0.05	-1.04	0.9430
12 – 6	-0.07	-1.50	0.7470
12 – 10	-0.02	-0.45	0.9990

Table 4.2. Multiple pairwise comparisons of chicks' pecking responses to SS of different diameters. * - S.E. = 0.05. Significant values in bold.

4.2b Assessing the effect of superstimulus stripe number and width

4.2bi Choice of three stripes or no stripes

As only 10 chicks took part in this trial, no distinction was made on the basis of how many times each chick pecked. For each stripe thickness, the striped arm was significantly preferred over the red arm (Table 4.3).

Stripe width (mm)	No. pecks – stripes	No. pecks – no stripes	*p*
1	13.60 ± 2.03	1.00 ± 0.63	**0.0044**
2	14.20 ± 2.56	3.00 ± 1.02	**0.0136**
3	16.30 ± 1.61	1.40 ± 0.54	**0.0014**
6	16.10 ± 1.62	1.40 ± 0.56	**0.0022**

Table 4.3. Chick pecking responses in experiment 4.2bi. The arm of the stimulus with three stripes was significantly preferred to that without stripes (the red arm) for all stripe widths tested. Significant values in bold.

4.2bii Choice of multiple stripes or no stripes

Again no distinction was made between the pecking behaviour of chicks in this trial, as only ten took part. In each case, the striped arm was preferred over the plain red arm (Table 4.4).

Stripe width (mm)	No. pecks – stripes	No. pecks – no stripes	*p*
1	10.10 ± 1.60	0.60 ± 0.31	**0.0012**
2	13.00 ± 1.90	1.00 ± 0.45	**0.0028**
3	14.70 ± 1.68	1.60 ± 0.54	**0.0020**
6	13.00 ± 0.29	1.00 ± 0.68	**0.0018**

Table 4.4. Chick pecking responses in experiment 4.2bii. The arm of the stimulus with multiple stripes was significantly preferred to that without stripes (the red arm) for all stripe widths tested. Significant values in bold.

4.2biii Choice of three stripes of different widths

Chicks' choices were split into those that pecked less than 15 times per trial (n = 22), those that pecked between 15 and 20 times per trial (n = 14), and those that pecked more than 20 times (n = 9). In all but the final of these categories, chicks significantly preferred the arm with the wider stripes when given the choice between 1 mm stripes and 2 mm stripes (Table 4.5). No preference was seen in any category when chicks were given the choice between 2 mm and 3 mm stripes (Table 4.5). In the choice between 3 mm and 6 mm stripes, the 3 mm stripes were preferred by all but the most prolific peckers (Table 4.5).

Stripe width choice (mm)	Chick category (pecks/30 s)	No. pecks – thin stripes	No. pecks – thick stripes	*p*
1 v 2	< 15	3.27 ± 0.71	8.68 ± 1.10	**0.0010**
	15 – 20	6.14 ± 1.10	14.29 ± 1.80	**0.0123**
	> 20	11.67 ± 1.98	14.78 ± 1.97	0.4671
2 v 3	< 15	6.29 ± 0.95	7.52 ± 0.84	0.1466
	15 – 20	9.57 ± 0.82	10.00 ± 1.41	0.4338
	> 20	12.33 ± 1.43	12.11 ± 1.52	0.9710
3 v 6	< 15	7.86 ± 0.91	5.36 ± 0.89	**0.0381**
	15 – 20	13.57 ± 1.57	7.93 ± 0.86	**0.0099**
	> 20	13.56 ± 2.76	11.00 ± 1.96	0.5899

Table 4.5. Chick pecking responses in experiment 4.2biii. There was an overall trend for chicks to prefer stripes of 2 – 3 mm. Significant values in bold.

4.2biv Choice of multiple stripes of different widths

Chicks were again separated in three groups: those that pecked less than 10 times per trial (n = 17), those that pecked between 10 and 15 times per trial (n = 7), and those that pecked more than 15 times (n = 11). For the choice between 1 mm and 2 mm stripes, chicks showed an overall preference for the thicker stripes, although this trend only approached significance for the least prolific peckers (Table 4.6). This overall trend was again seen for the choice between 1 mm and 3 mm stripes, although this time there was no significant preference for the chicks that pecked the least, an almost significant preference for the thicker stripes in the intermediate chicks, and a significant preference for the 3 mm stripes in the chicks that pecked the most (Table 4.6). In the choice between 2 mm and 3 mm stripes, there was no preference overall, although the most prolific peckers almost expressed a significant preference for the 2 mm stripes (Table 4.6). There was no significant difference between the number of times chicks chose between the 3 mm striped arm, and the 6 mm stripes (Table 4.6).

Stripe width choice (mm)	Chick category (pecks/30 s)	No. pecks – thin stripes	No. pecks – thick stripes	*p*
1 v 2	< 10	3.40 ± 0.79	4.80 ± 1.03	0.0831
	10 – 15	6.86 ± 1.47	11.14 ± 1.16	**0.0156**
	> 15	6.64 ± 0.98	13.55 ± 1.35	**0.0090**
1 v 3	< 10	4.06 ± 1.25	3.88 ± 0.74	0.2992
	10 – 15	7.29 ± 2.15	13.71 ± 2.39	0.0819
	> 15	8.45 ± 1.00	12.82 ± 1.20	**0.0223**
2 v 3	< 10	5.06 ± 1.30	3.63 ± 0.67	0.1740
	10 – 15	6.71 ± 1.77	8.86 ± 1.50	0.2574
	> 15	14.45 ± 1.75	9.18 ± 1.35	0.0566
3 v 6	< 10	5.81 ± 1.15	5.13 ± 0.93	0.3143
	10 – 15	10.00 ± 1.27	8.71 ± 2.00	0.3435
	> 15	14.45 ± 2.47	10.91 ± 1.78	0.1906

Table 4.6. Chick pecking responses in experiment 4.2biv. There was a tendency for chicks to prefer stripes of 2 – 3 mm. Significant values in bold.

4.2bv Choice of three stripes or multiple stripes

Chicks in this trial were divided into those that pecked fewer than 10 times (n = 19), those that pecked between 10 and 20 times (n = 12), and those that pecked more than 20 times (n = 15). In the trial with 1 mm striped arms, the chicks in the first two categories showed a preference (only significant for the intermediate chicks) towards the fully striped arm (Table 4.7), while the chicks that pecked the most preferred the arm with only three stripes (Table 4.7). There was no overall preference between arms for the 2 mm thick stripes (Table 4.7), the 3 mm stripes (Table 4.7) or the 6 mm stripes (Table 4.7).

Stripe width (mm)	Chick category (pecks/30 s)	No. pecks – three stripes	No. pecks – multiple stripes	*p*
1	< 10	3.68 ± 0.74	5.47 ± 1.09	0.0614
	10 – 20	5.75 ± 1.03	9.83 ± 1.35	**0.0449**
	> 20	14.94 ± 1.54	10.07 ± 1.14	**0.0267**
2	< 10	3.00 ± 1.07	4.37 ± 0.83	0.1705
	10 – 20	8.67 ± 1.22	10.00 ± 1.15	0.2871
	> 20	12.67 ± 1.00	13.27 ± 1.03	0.3898
3	< 10	4.47 ± 1.11	3.74 ± 0.93	0.3081
	10 – 20	8.58 ± 1.26	8.33 ± 1.55	0.4740
	> 20	13.87 ± 1.47	12.53 ± 1.04	0.3073
6	< 10	3.89 ± 0.75	4.42 ± 0.95	0.3363
	10 – 20	8.75 ± 1.05	7.58 ± 1.12	0.2720
	> 20	14.60 ± 1.21	12.20 ± 1.28	0.1121

Table 4.7. Chick pecking responses in experiment 4.2bv. In the majority of cases, chicks did not appear to distinguish between the arm of the stimulus with three stripes, and that with multiple stripes. Significant values in bold.

4.2c Isolating the effect of individual features of the superstimulus

Only stimulus type had a significant effect on chick pecking behaviour (LMM, $F_{5,105} = 16.51$, $p < 0.0001$) (Fig. 4.11). *Post-hoc* tests showed that this effect was due to the SS, with 20.91 ± 1.02 pecks per 30 s, eliciting a significantly greater number of pecks than the Control (10.41 ± 1.49), Red (13.94 ± 1.47), Long (11.05 ± 1.27), or Thin (10.50 ± 1.28) models. Stripes (17.09 ± 1.74) also provoked significantly more pecks than the Control, Long and Thin stimulus types (Table 4.8).

Comparison	Estimate*	Z	*p*
Long – Control	0.64	0.44	0.9979
Red – Control	3.55	2.46	0.1376
SS – Control	10.50	7.27	**<0.0001**
Stripes – Control	6.68	4.63	**<0.0001**
Thin – Control	0.09	0.06	1.0000
Red – Long	2.91	2.02	0.3338
SS – Long	9.86	6.83	**<0.0001**
Stripes – Long	6.05	4.19	**<0.0001**
Thin – Long	-0.55	-0.38	0.9990
SS – Red	6.96	4.82	**<0.0001**
Stripes – Red	3.14	2.17	0.2510
Thin – Red	-3.46	-2.39	0.1588
Stripes – SS	-3.82	-2.64	0.0868
Thin – SS	-10.41	-7.21	**<0.0001**
Thin – Stripes	-6.59	-4.57	**<0.0001**

Table 4.8. LMM pairwise comparisons of mean estimates. *p*-values adjusted for multiple comparisons. * S.E.=1.44. Significant differences in bold.

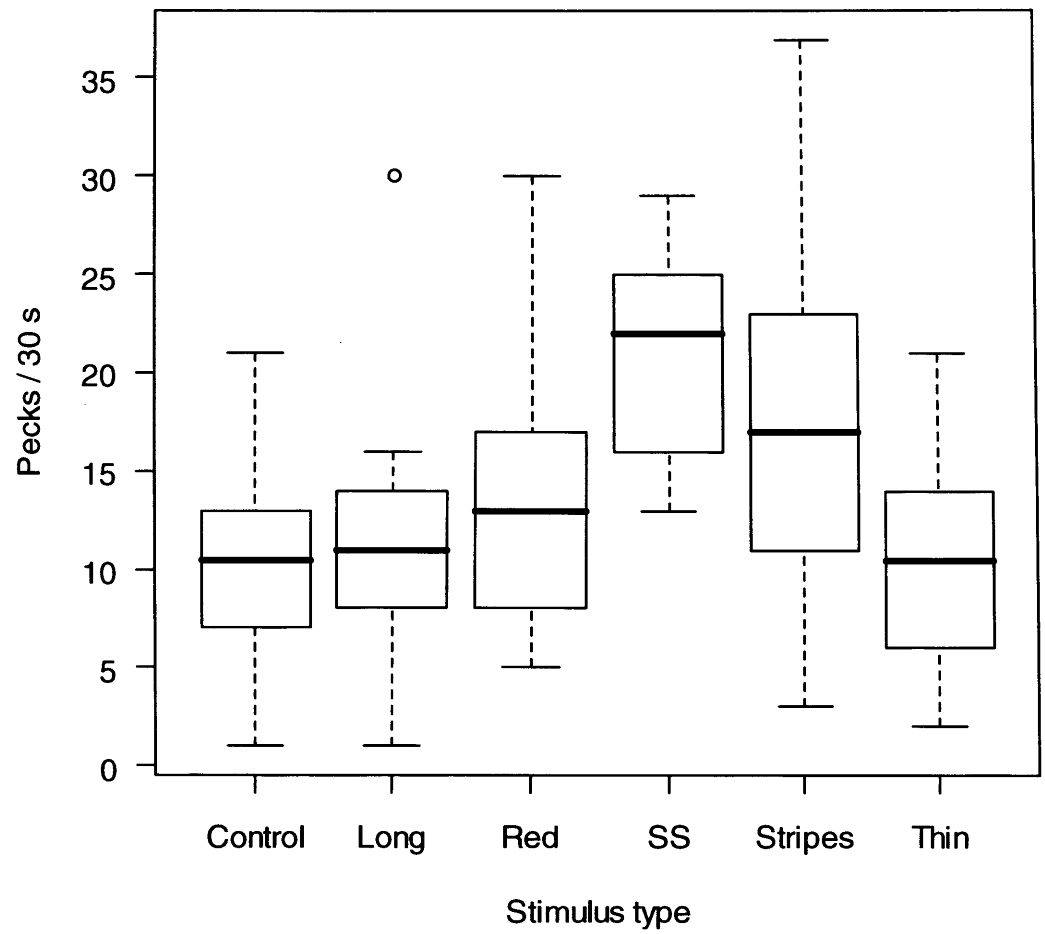

Fig. 4.11. The relationship between stimulus type and chick pecking response in experiment 4.2c. Following the SS, the Stripes and then the Red stimuli were the most attractive to chicks.

A significantly higher proportion of pecks were aimed at the gonys spot for the Control model (81.2%) than for the Long (71.2%) (GLMM, $z = -2.99$, $p = 0.0028$), Red (73.0%) (GLMM, $z = -2.24$, $p = 0.0251$) and Thin (67.1%) (GLMM, $z = -3.37$, $p < 0.0001$) models. There was no significant difference between the proportion of pecks aimed at the gonys spot on the Control and Stripes (85.6%) models. Of the pecks directed away from the gonys spot, the highest proportion (37.2%) was to the eye for the Control model. The eye was also the most popular destination for "stray" pecks in the Thin (38.2%), the Red (51.0%) and the Stripes (53.7%) stimulus types. This feature received no pecks at all in the Long model. The gape received 16.3% of "stray" pecks for the Controls, 4.3% for the Longs, 27.6% for the Thins, 24.1%

for the Stripes and 7.3% for the Reds. Of the stray pecks to the Long head, 87.1% were to parts of the beak other than the gonys spot.

4.2d Deleting individual features of the superstimulus

Stimulus type had a significant effect on chicks' rate of pecking (LMM, $F_{5,100} = 9.79$, $p < 0.0001$) (Fig. 4.12). Pairwise comparisons of the factor levels showed that LTR (14.05 ± 1.22) elicited significantly fewer pecks than the Control (20.09 ± 1.55), LRS (22.27 ± 1.47), SS (21.95 ± 1.12) and TRS (18.86 ± 1.55). LTS (17.64 ± 1.52) also elicited a smaller number of pecks than LRS or SS (Table 4.9).

Comparison	Estimate*	*z*	*p*
LRS - Control	2.18	1.52	0.6522
LTR - Control	-6.05	-4.21	**<0.0001**
LTS - Control	-2.45	-1.71	0.5260
SS - Control	1.86	1.30	0.7868
TRS - Control	-1.23	-0.85	0.9571
LTR - LRS	-8.23	-5.73	**<0.0001**
LTS - LRS	-4.64	-3.23	**0.0159**
SS - LRS	-0.32	-0.22	0.9999
TRS - LRS	-3.41	-2.37	0.1658
LTS - LTR	3.59	2.50	0.1241
SS - LTR	7.91	5.51	**<0.0001**
TRS - LTR	4.82	3.35	**0.0104**
SS - LTS	4.32	3.01	**0.0317**
TRS - LTS	1.23	0.85	0.9571
TRS - SS	-3.09	-2.15	0.2610

Table 4.9. Pairwise comparisons of mean estimates. *p*-values adjusted for multiple comparisons. * S.E.=1.44. Significant values in bold.

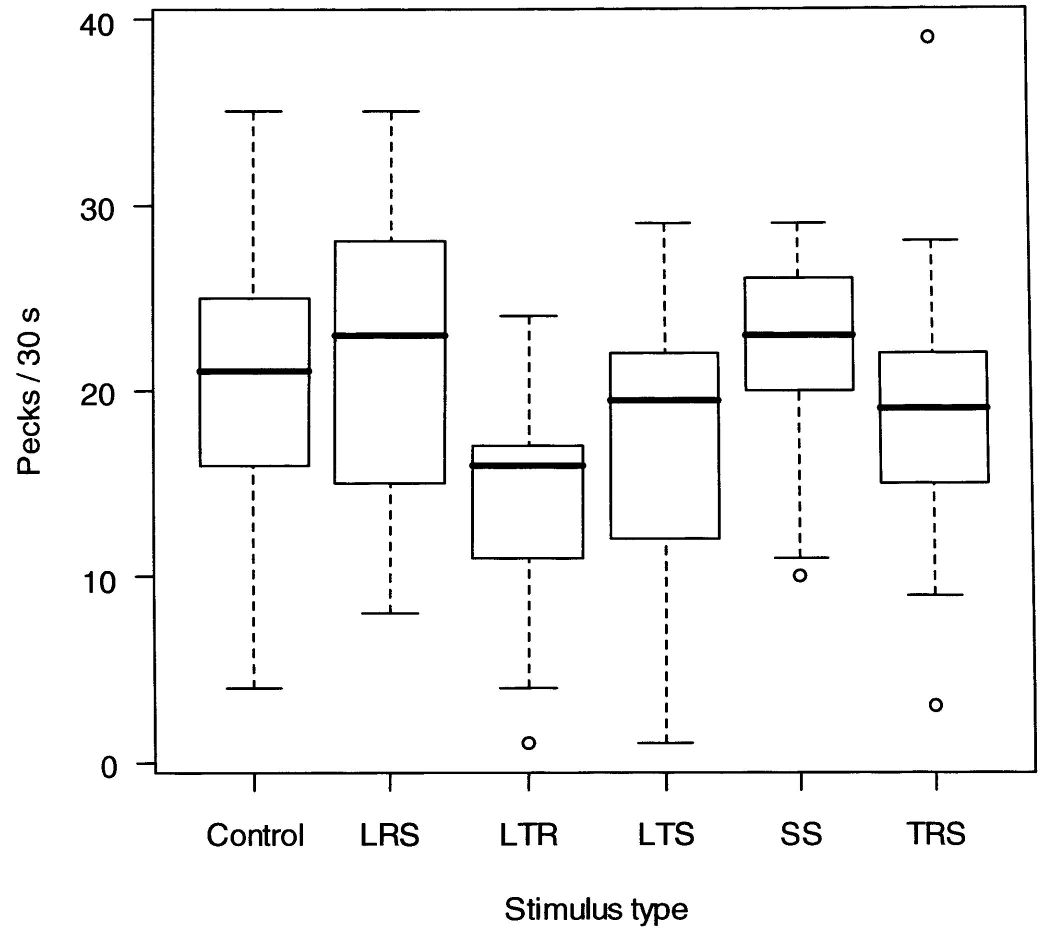

Fig. 4.12. The relationship between stimulus type and chick pecking response in experiment 4.2d. Stripes appears to be the strongest element of the SS, as its elimination causes the weakest chick response.

Order of stimulus presentation was again significant (LMM, $F_{5,100} = 2.43$, $p = 0.0398$), with chicks showing a trend towards habituation as the trials progressed.

Examination of the position of chicks' pecks showed that 62.3% were directed towards the gonys spot for the Control model, against 66.7% for LTR, 88.4% for LRS, 84.0% for LTS and 53.5% for TRS. There was no significant difference in this behaviour for the Control and LTR, but compared to the Control, a significantly greater proportion of the chicks' pecks went to the spot for LRS (GLMM, $z = 8.84$, $p < 0.0001$) and LTS (GLMM, $z = 6.60$, $p < 0.0001$), while a significantly smaller proportion hit the spot for TRS (GLMM,

$z = -2.54$, $p = 0.0112$). A very small proportion of the "stray" pecks were aimed at the gape for any of the models (Control - 7.9%, LTR – 5.8%, LRS – 3.5%, LTS – 1.6%, TRS – 6.2%). Many of these pecks were instead directed at the eye (Control – 79.4%, LTR – 35.9%, LRS – 22.8%, LTS – 37.1%, TRS – 66.3%).

Experiment 4.3 – External and intrinsic effects on the supernormal pecking response

4.3a Effect of extrinsic factors on supernormal pecking

Sexing was carried out on 10 chicks, seven of which were successfully sexed (Fig. 4.13). However, this was not enough to construct a meaningful model of sexual differences in the pecking response. PCRs showed high levels of degradation in the DNA, probably due to the storage method. Results were also inconsistent, with the sex of several chicks changing between PCRs, indicating allelic dropout (Bantock *et al.*, 2007). It was thus decided not to pursue PCRs on the other extracted samples because of the time and expense concerned.

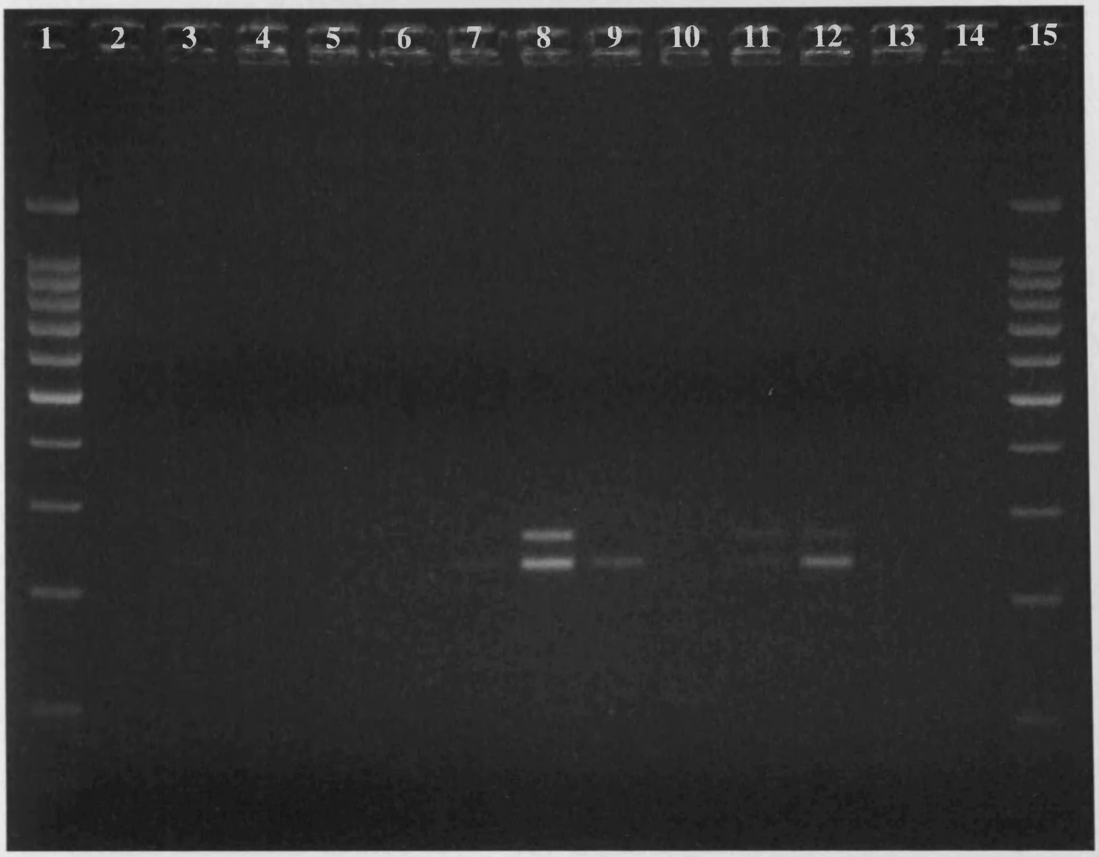

Fig. 4.13. Results of a sexing PCR. Two bands = female. One band = male. Lanes 1 (far left) and 15 (far right) contain size standard DNA showing 100 bp intervals.

Two explanatory variables had a significant effect on chick pecking rate. The first of these was egg volume (GLM, $F_{1,48} = 4.43$, $p = 0.0406$), with chicks from larger eggs responding with a significantly greater pecking rate towards the SS. The effect of laying order also approached significance ($F_{2,48} = 2.82$, $p = 0.0694$). It was retained in the model because when deleted, the likelihood ratio test statistic became significant ($F_1 = 4.43$, $p = 0.0172$) and the AIC increased from 171.82 to 176.63. Contrasts showed that both B chicks and C chicks pecked at a significantly greater rate than A chicks ($t_{3,48} \geq 2.30$, $p \leq 0.0257$ and $t_{3,48} = 2.30$, $p = 0.0406$ respectively). However, the effect sizes for both egg volume and laying order were small, and the model had little overall explanatory power, with an adjusted R^2 of 12.18%

4.3b Supernormal pecking and stimulus experience

Simplification of models left chick age as the only significant predictor of chick pecking behaviour (GLM, $F_{1,83} = 16.47$, $p = 0.0001$), with an increase in pecking rate towards the SS as chicks get older (Fig. 4.14). The explanatory power of this model was weak, with an adjusted R^2 of 15.55%.

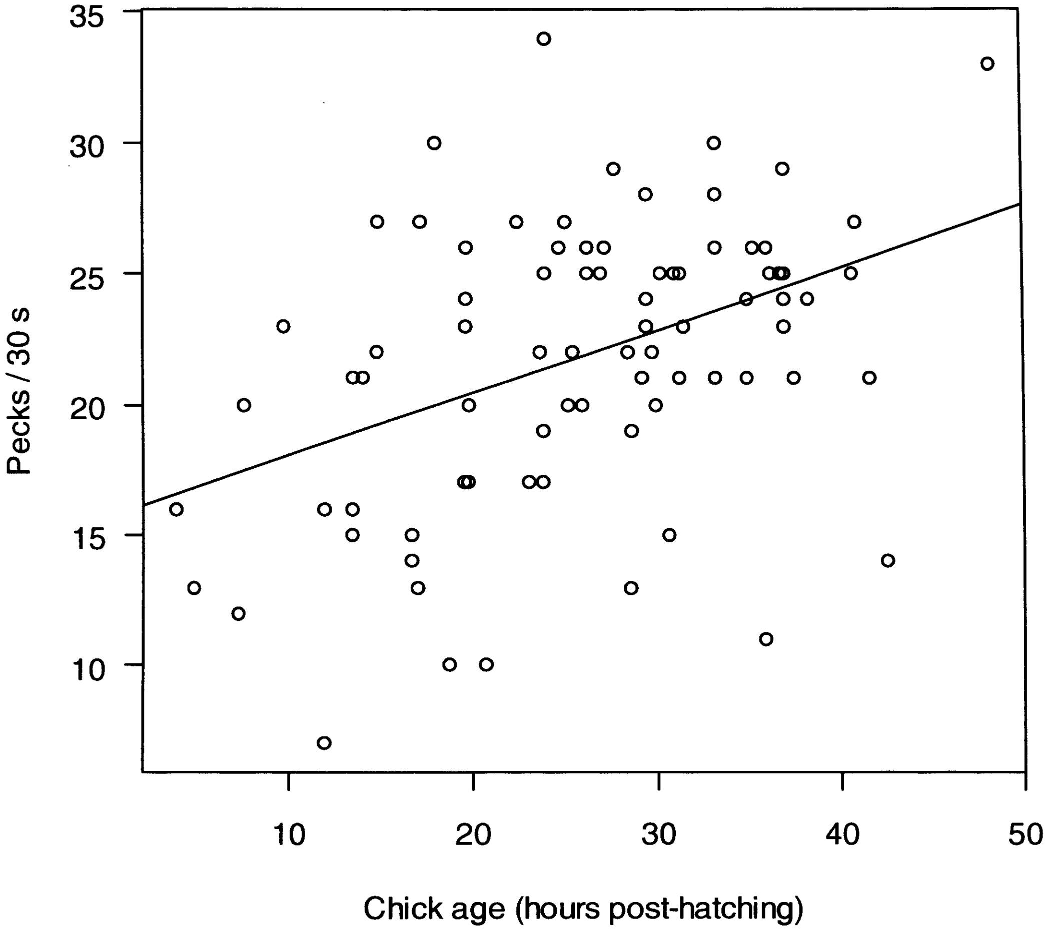

Fig. 4.14. The relationship between chick age and supernormal pecking response. Chick pecking response increased significantly with age.

4.4 DISCUSSION

4.4.1 The supernormal effect

The results of the experiments described in this chapter confirm that a significant supernormal pecking response is indeed found in Lesser Black-backed Gull chicks. Although Tinbergen and Perdeck (1950) did not statistically assess the supernormal response they described in Herring Gull chicks, it appears that this behaviour is essentially identical to that found in Lesser Black-backed Gull chicks, indicating that it is highly conserved amongst the large white-headed gull species group (Fig. 1.1).

Inspection of the characteristics of the SS bringing about the supernormal response indicated that the optimum diameter of this stimulus is around 3 - 4.5 mm (experiment 4.2a). This falls within the optimal range found in Black-headed Gull chicks, which pecked preferentially at rod-stimuli of 2 - 10 mm in diameter (Weidman, personal communication, in Cullen, 1962), although it is smaller than the 9 mm diameter favoured by Laughing Gulls (Hailman, 1962). All sizes of SS were significantly more effective at provoking a response than the 1 mm stimulus, indicating either that chicks are not interested in such narrow objects, or that they have trouble seeing them, or focussing their pecks on them. Chicks' responses also tailed off as stimulus diameter increased to 10 mm, indicating that above this size, the supernormal component associated with the width loses its effectiveness.

The results of the choice trials (experiment 4.2b) showed an overall preference for stripes of 2 - 3 mm in width. The 6 mm stripes were less attractive than the 2 and 3 mm stripes when only three stripes were on offer. When both arms were fully striped, this trend disappeared. Although there was a definite preference for stripes over none, chicks did not show any strong preference between arms with three stripes and arms that were fully striped. The preferred widths in these experiments are similar to those selected for the diameter of the SS experiment 4.2a, with widths of 1 mm again emerging as relatively ineffective at releasing pecking. Perhaps therefore, chicks' nervous systems are attuned to detect objects of approximately 3 mm in width or diameter.

The addition of a single feature of the SS to Control-like models (experiment 4.2c) indicated that the three white stripes were the most powerful element of this stimulus. The Stripes model was both significantly more attractive to the chicks than all others except the Red, and the only model that was not significantly less effective at eliciting pecks than the SS (although this difference approached significance at $p = 0.0868$). The raw values and lack of significant difference between the Stripes and Red models imply that the red colour is the next most important element of the SS. The raw values also indicate alterations to the bill's shape (i.e. the Long and Thin stimuli) have little effect on the supernormal response relative to the Control.

Elimination of a single element of the SS (experiment 4.2d) appeared to confirm these trends. The model without stripes (LTR) received the smallest number of pecks, and the difference between the levels of pecking elicited by this model and the others was significant for all models except LTS. The fact that LTS (the model with the red colour eliminated) was the next least effective stimulus again indicates that red is the second most important attribute of the SS, and that the exaggerated length and thinness are the least important features, as they were common to the two least attractive stimuli. The most attractive stimulus, LRS, had both the red colour and the three white stripes, and was as attractive as the SS itself in terms of both raw values and significant differences with other stimuli (only the LRS and the SS provoked significantly more pecks than LTS). Since LRS not TRS was the most effective stimulus, it could be inferred that elongation is more important than narrowness in eliciting the supernormal response.

Interestingly, there appears to be heterogeneous summation between the four elements of the SS (red, stripes, long, thin), whereby the response to the Control plus each of the elements in isolation, sums together to give the total pecks delivered to a stimulus featuring all components (i.e. the SS). The mean difference in the response to the Control and to the SS was 10.50 pecks per 30 seconds. Adding up the differences between all the other stimuli and the Control gives 10.95 pecks per 30 seconds. This is reminiscent of the finding that chicks' responses to the releasers of the "normal" pecking response (the adult bill's colour and shape in the case of Laughing Gulls, and bill colour, shape and gonys spot in American Herring Gulls) heterogeneously sum to give the pecking response to a complete adult head stimulus (Margolis *et al.*, 1987; Alessandro *et al.*, 1989).

This effect did not operate in the opposite direction, however – there was no "heterogeneous deletion" effect. Chicks' responses to all the stimuli in this set of behavioural tests were high compared to responses recorded in the other experiments (experiments 3.4, 4.1, 4.2c and 5.2), with overall pecking rates to each stimulus similar to levels received by the SS in all other experiments. This suggests that once a certain number of elements of the SS are present, chicks pass the threshold of maximal stimulation and their pecking response becomes almost as strong as that to the SS itself.

Since chicks pecked at a similar rate towards the Ventral and Control models (experiment 4.1), there was no support for Tinbergen and Perdeck's (1950) hypothesis that chicks show an exaggerated response to the SS because it resembles the chick's view of the parent's bill from below. Had this been the case, the results might have shown a preference for the Ventral model over that of the Control, placing it on a continuum from Control to SS. However, the finding that significantly fewer pecks to the Ventral model were aimed away from the gonys spot than for the Control does suggest that chicks peck the gonys spot more accurately when it is viewed from below, instead of being distracted by other features such as the parent's eye. Perhaps, therefore, there is something in the idea that the chick's innate behaviour is more attuned to being fed by parents at this angle, though not in the way that Tinbergen and Perdeck (1950) suggested.

4.4.2 Factors affecting the supernormal response

Few factors emerged as significant in the experiments apart from the nature of the stimulus presented to the chicks. The order of stimulus presentation was significant in two sets of behavioural tests, each time indicating habituation during the course of the experiment. This backs up Tinbergen and Perdeck's (1950) own observation of "negative conditioning" upon repeated exposure to stimuli. However, unlike this study, and subsequent work (Nyström, 1973; ten Cate *et al.*, 2009), the experiments described here show a decline in responsiveness during tests in which chicks were presented with each stimulus type on a single occasion, and when they were given relatively lengthy breaks between trials. This suggests that chicks were habituating to the environment in which experiments were carried out[35] rather than to the stimuli, as in both cases the models used were dissimilar to each other, and again underlines how sensitive this form of innate behaviour is to modification through experience.

An increase in the supernormal pecking response with age was also found in two separate analyses. This trend conforms with similar observations of an improvement in pecking rate with age in Black-headed gulls (Weidmann & Weidmann, 1958) and Ring-billed Gulls (*L. delawarensis*) (Iacovides & Evans, 1998). However, compared to the latter study, the findings of this chapter demonstrate an effect in younger chicks. The increase in response with chick age is probably due to improved motor coordination of older chicks (Hailman, 1967) together with increasing levels of hunger, though within the age range used, chicks would still have had ample yolk reserves (Hailman, 1967; Hario *et al.*, 2004), and they are often not fed by their parents until they are several hours old (Tinbergen & Perdeck 1950, personal observation). The significant interaction effect between stimulus type and age in the test of Tinbergen and Perdeck's (1950) hypothesis (experiment 4.1) indicates that the supernormal effect is less pronounced in very young chicks, but intensifies with age.

The remaining factors (egg volume and laying order) that significantly affected chicks' supernormal responses only came to light when a large sample size (52 chicks) was considered, as the effect size of each was small. Chick pecking rate increased with egg volume, echoing a similar finding in the relationship between egg mass and pecking towards a Control-like stimulus in Yellow-legged Gulls (Alquati *et al.*, 2007). The egg volume effect could be

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[35] Chicks in the wild learn characteristics of their nest sites soon after hatching (Noseworthy & Lien, 1976).

explained by the larger yolk reserves of chicks from bigger eggs (Parsons, 1970), providing these individuals with more energy for pecking. Chicks from larger eggs have also been shown to be in better condition and larger skeletally than those from smaller eggs (Bolton, 1991), indicating again that they might be physically stronger and hence better able to peck (section 3.1.2.1).

The laying order effect was very weak, but indicated that A chicks were less inclined to peck than B and C chicks. This could be explained by intraclutch differences in yolk hormones (section 3.1.2.1), but it is perhaps equally likely to be a spurious result, especially considering that the results of most other studies have singled out C chicks from the rest of the brood, rather than A chicks (e.g. Parsons, 1970; Hario & Rudbäck, 1999; Muck & Nager, 2006). Assuming there was no true effect of laying, as it was not found in any of the other experiments in this chapter or in Chapters 3 and 5, this result would contradict that of a study showing a decrease in pecking response with laying order in Yellow-legged Gulls (Alquati *et al.*, 2007). However, it would be in keeping with the findings of Boncoraglio *et al.* (2006), who found that manipulation of yolk testosterone levels, which have been shown to increase with laying order (Royle *et al.*, 2001; Groothuis & Schwabl, 2002), did not significantly effect the pecking rate of young chicks towards a two-dimensional model of an adult head. Similarly, Smith *et al.* (2005) found that begging intensity did not vary with hatching order (which usually equates to laying order (Parsons, 1975a)) in Common Terns (*S. hirundo*).

4.4.3 The adaptive significance of the supernormal response

The results presented here found little support for Tinbergen and Perdeck's (1950) explanation of the mechanism behind the supernormal response. This could have been partly due to reasons discussed in section 4.1.3, namely the fact that supernormal pecking is found in gull species without a red gonys spot, and that it is not guaranteed that chicks would view their parents' bills from beneath. Tinbergen and Perdeck (1950) themselves said that chicks would only view their parents from this angle the very first time they were fed, and argued that the supernormal response was adaptive purely to this first feeding. However, this statement does not account for their own observations that this behaviour persists in older chicks, and the results presented here show that it even increases in magnitude with age.

There is also little support for the hypothesis that chick pecking is adapted to parental bill colour, and that it is thus a resemblance with the bill that accounts for supernormal preferences for exaggerated objects of that colour (Cullen, 1962). The presence of the three white stripes was the strongest releasing element of the SS by a considerable margin, but such a feature is not seen in the large white-headed gulls, or indeed the Laridae is a whole. However, a black stripe occurs in certain species (e.g. the Ring-billed Gull, *L. delawarensis*), and both a white bill tip and upper proximal bill spot (thought to be an adaptation to nocturnal feeding (Hailman, 1964)) is found in the Swallow-tailed Gull (*Creagrus furcatus*). This, along with the presence of a white bill stripe in a fellow member of the Lari, the Razorbill (*Alca torda*), suggests that white bill stripes could have arisen in gulls had suitable selection pressure existed.

Although the results of experiment 4.2c, in which the addition of three white bill stripes to a Control model increased pecking to supernormal levels, might suggest that the evolution of bill stripes could confer a selective advantage in terms of facilitating chick feeding, it might in fact be disadvantageous to over-stimulate begging chicks. This is due to the energetic cost to chicks of sustained pecking at a high rate, and because such attractive bill stimuli might impede the necessary switch in chicks' attention from the bill to regurgitated foodstuffs. (As demonstrated in experiment 5.2, although the gonys spot is ordinarily the focus of pecking, objects in the bill tips effectively divert chicks' pecking away from the spot).

The bill features that have evolved in larids might also be more adaptive than white stripes would be, because of their dual role in imparting information about individual quality as well as in chick feeding (Morales *et al.*, 2009).

Larid bill markings are typically mediated by carotenoid and melanin pigments, which are sensitive to changes in individual condition (Blount *et al.*, 2002; Kristiansen *et al.*, 2006; Møller *et al.*, 2007; Pérez *et al.*, 2008), thus serving as a sexual signal in addition to promoting chick feeding. White stripes might not be able to convey such messages about phenotypic quality.

The question therefore remains - why does the supernormal pecking response exist? Although the results cannot rule out non-adaptive pre-existing sensory biases (Ramachandran, 2004), they do provide some indication that the SS is attractive because it taps into innate foraging preferences. The strength of the white stripes over the other SS features could reflect the segmented and/or scaled nature of the soft-bodied prey eaten by young at the early chick stage. A recent study has reported the widespread consumption of segmented earthworms (Lumbricidae) by Lesser Black-backed Gulls in the breeding season (Coulson & Coulson, 2008b), and observations of regurgitates on Flat Holm revealed the prevalence of reddish, segmented ragworms (*Hediste* spp.) in the diet of young chicks (Stanworth, 1998; personal observation) (Fig. 4.15). The presence of worms and insects in the breeding season diet has also been recorded in a number of other gull species (e.g. Götmark, 1984; Brown & Ewins, 1996) (section 5.16), and dietary switches to small, segmented or scaled foodstuffs (i.e. worms or small fish) have been observed during the early chick stage in several species (Table 5.2). It could be argued that the absence of a preference for several stripes over only three stripes in experiment 4.2b contradicts these inferences, since worms in particular have more than three segments. However, as chicks' food is frequently regurgitated in a mass (Fig. 4.15), the form and orientation of many of the prey items contained therein might be obscured. Therefore, chicks might have been selected to be sensitive to the presence of only a small number of clearly visible stripes, such that this alone is sufficient to invoke food recognition.

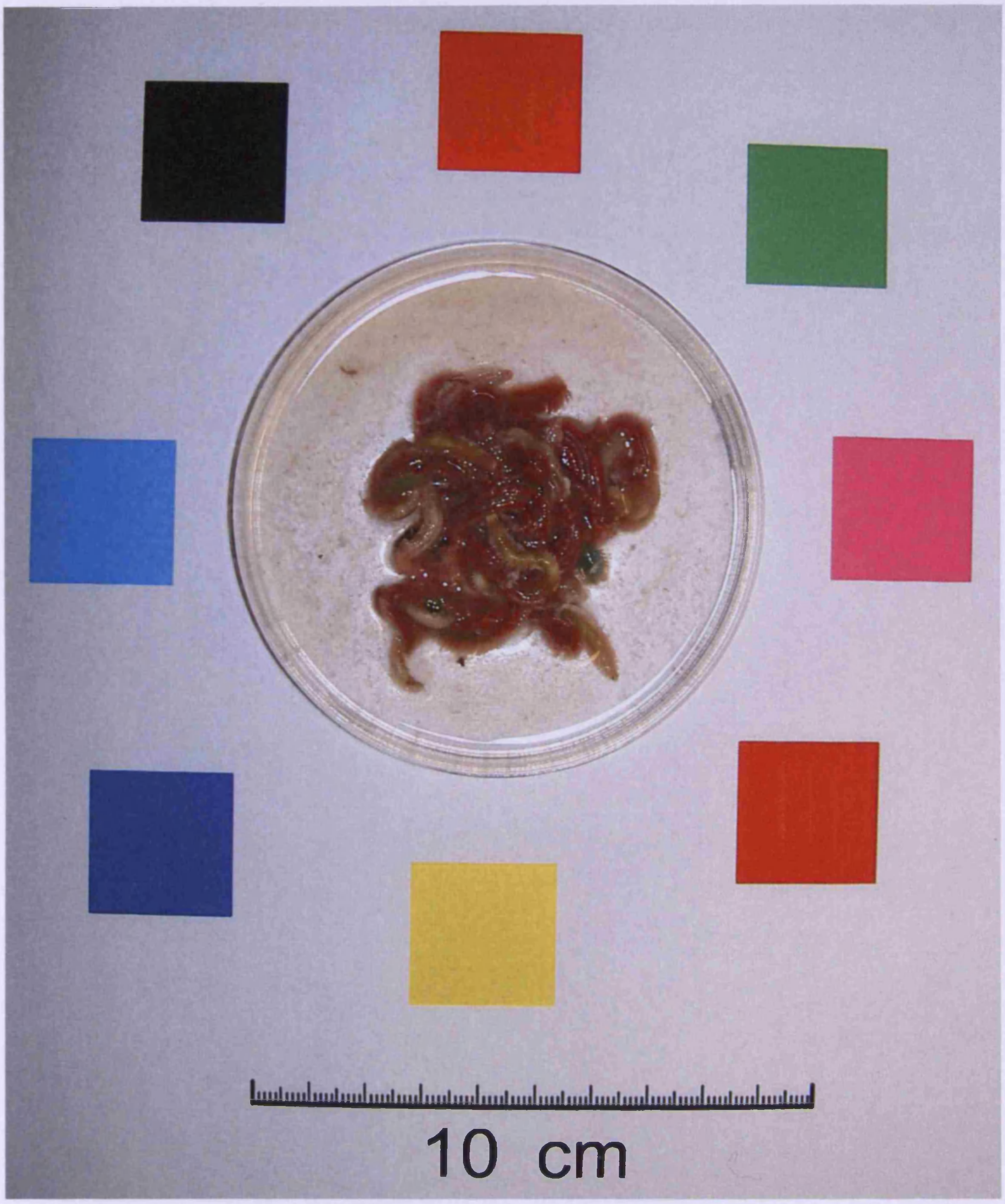

Fig. 4.15. Regurgitate of a one-day old Lesser Black-backed Gull chick, Flat Holm, 23rd May 2006.

Chicks' pecks to their parents' gonys spot in the Lesser Black-backed Gull and related species might therefore provide a signal to parents to initiate the dietary switch for feeding newly hatched chicks. The spot would thus play an important role in facilitating parent-chick communication about feeding, while chick supernormal pecking behaviour, observed in species with a range of adult bill markings, would instead reflect the preferences of young for foodstuffs which are delivered to them early in life.

Chapter 5

Experimental investigation of food recognition and feeding preferences in hatchling Lesser Black-backed Gulls (*Larus fuscus*)

5.1 INTRODUCTION

Gull chicks depend fully on their parents for food (O'Connor, 1984; Starck & Ricklefs, 1998), inducing their parents to regurgitate through innately mediated pecks to their bills in a process known as the pecking response (Tinbergen & Perdeck, 1950; Hailman, 1967). This behaviour has been the subject of several studies (reviewed in Chapter 3). The process by which gull chicks recognize food items, and switch their attention from pecking their parents' bills to pecking at food, is less well studied or understood. Gull chicks, in common with the young of most birds, are often reared on diets that are significantly different from the normal intake of adults (O'Connor, 1984). It has been shown that departures from the optimal food types required by chicks can have adverse effects on their growth, development and survival (e.g. Murphy *et al.*, 1984; Bukacińska *et al.*, 1996). Such dietary needs could have given rise to selection for an ability in chicks to recognize and seize particular food items preferentially, similar to the innate recognition of parental bill features displayed in the pecking response.

5.1.1 Diet of adult gulls

In many parts of the world, gulls have colonized a range of environments, including urban areas. They have thus developed a reputation as noisy pests (Monaghan & Coulson, 1977; Rock, 2005), which pose a risk to public health and a danger of bird strike at airfields (Mudge, 1978; Mudge & Ferns, 1982; Belant *et al.*, 1993; Furness & Monaghan, 1987; Raven & Coulson, 1997; Yorio *et al.*, 1998; Ferns & Mudge, 2000; Soldatini *et al.*, 2008). They may also impact negatively on ecological communities and on populations of other species (Tinbergen, 1953; Sobey, 1986; Furness & Monaghan, 1987; Skórka *et al.*, 2005; but see Spaans, 1971; Payne & Moore, 2006; Oro & Martínez-Abraín, 2007). One of the reasons that gulls are able to successfully inhabit such diverse habitats is that many species can persist on a wide range of food items (Tinbergen, 1953; Harris, 1965; Threlfall, 1968; Spaans, 1971; Hunt & Hunt, 1973b; Mudge & Ferns, 1982; Sibly & McCleery, 1983a; Götmark, 1984; Furness & Monaghan, 1987; Pierotti & Annett, 1987). Gulls are typically both opportunist and generalist in their foraging habits (Trapp, 1979; Sibly & McCleery, 1983a; Bertellotti & Yorio, 1999; Kubetzki *et al.*, 1999), rapidly changing their diet and their means of obtaining food in response to fluctuations in availability (Oro, 1996b; Oro *et al.*, 1997; Schwemmer & Garthe, 2008).[36]

Gulls have therefore benefited from the increase in urbanization among human populations over recent decades, and the concurrent rise in edible refuse (e.g. Tinbergen, 1953; Fordham & Cormack, 1970; Hickling, 1977; Horton *et al.*, 1983; Coulson *et al.*, 1987; Sol *et al.*, 1995; Auman *et al.*, 2008). The widespread adoption of waste disposal at landfill sites since the 1950s has proved particularly advantageous for gulls, as these areas provide a predictable and constant food supply (Horton *et al.*, 1983; Pons & Migot, 1995). As well as subsisting on general human-generated rubbish, gulls are adept at exploiting that from the fishing industry,[37] scavenging discards at ports (Harris, 1965; Ludynia *et al.*, 2005), inland fisheries (Hüppop & Hüppop, 1999) and tips (Haycock & Threlfall, 1975; Bertellotti *et al.*, 2001; Giaccardi & Yorio, 2004), in addition to following boats where they take bycatch and fish guts as these are thrown overboard (Tinbergen, 1953; Oro *et al.*, 1995; Kubetzki *et al.*, 1999; Yorio & Caille, 1999; Villablanca *et al.*, 2007)

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[36] Species that do not exhibit such flexibility in their feeding ecology, such as Olrog's Gull (*L. altanticus*), are not common in built up areas and are typically rare throughout their range (Delhey *et al.*, 2001; Beron *et al.*, 2007).

[37] Gulls can be adversely affected by commercial fishing activities, becoming tangled in lines and caught on baited hooks. This is a particular problem for the endangered Olrog's Gull (Beron *et al.*, 2007).

or dive for fish as these are gathered in the nets (Arcos & Oro, 2002). Gulls have even been known to take ornamental fish from lakes and ponds in parks and gardens, using bread thrown to feed the birds by passers by as bait (Henry & Aznar, 2006).

Feeding gulls also capitalize on farming activities. Terrestrial invertebrates such as earthworms, along with grain and small vertebrates, are obtained on arable fields; gulls can often be seen following agricultural machinery when fields are ploughed, harrowed, harvested or mowed, and dipping to the ground to capture prey as it is revealed (Vernon, 1972; Kirkham & Morris, 1979; Evans, 1982b; Welham, 1987; Coulson & Coulson, 2008b). Gulls also catch invertebrates in parks, golf courses and other man-made green areas. They sometimes achieve this by paddling, where the feet are rapidly and alternately stamped (Tinbergen, 1953; Delius, 1971), which attracts worms to the surface (Vernon, 1972; Brown & Ewins, 1996). Other anthropogenic food sources include abattoirs (Fordham & Cormack, 1970; Nogales *et al.*, 1995; Yorio *et al.*, 1998), road-kill (Coulson & Coulson, 2008b), and effluent and the resulting biota at sewage works and outfalls (Vernon, 1972; Hunt & Hunt, 1973b; Mudge & Ferns, 1982; Yorio *et al.*, 1998; Ferns & Mudge, 2000; Raven & Coulson, 2001). The quantity and diversity of food supplied through human activities is thought to have contributed to a marked increase in several gull populations since the mid-twentieth century (Brown, 1967b; Spaans, 1971; Kihlman & Larsson, 1974; Hickling, 1977; Mudge, 1978; Pons & Migot, 1995; Skórka & Wójcik, 2008),[38] as well as allowing several species to coexist sympatrically that might otherwise compete for limited natural resources (Hunt & Hunt, 1973b).

The techniques gulls use to exploit anthropogenic food sources are adapted from those evolved in more natural foraging situations. Gulls scavenge

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[38] Gull population increases are also due to protective measures implemented in the late nineteenth and early twentieth centuries, reducing hunting, egging and exploitation by the plumage trade (Kadlec & Drury, 1968; Spaans, 1971; Monaghan & Coulson, 1977; Mudge, 1978).

successfully on other mammalian, fish and avian species, consuming food remains and general detritus, including faeces, afterbirths and carcasses (Tinbergen, 1953; Moyle, 1966; Snow & Snow, 1969; Isenmann, 1976; Murphy *et al.*, 1984; Favero *et al.*, 1997; Suarez & Yorio, 2005; Gaston *et al.*, 2009). They also employ inter- and intraspecific kleptoparasitism (theft of food items already procured by another individual (Morand-Ferron *et al.*, 2007)) in both man-made and natural settings (Tinbergen, 1953; Harris, 1965; Verbeek, 1977a; 1979; Burger & Gochfeld, 1981b; Drexler Rockwell, 1982; Elston & Southern, 1983; Greig *et al.*, 1983; Hackl & Burger, 1988; Oro, 1996b; Bertellotti & Yorio, 2000; Skórka & Wójcik, 2008), along with inter- and intraspecific predation of eggs and chicks (Tinbergen, 1953; Brown, 1967a; Davis & Dunn, 1976; Trapp, 1979; Verlarde, 1987; Pierotti & Annett, 1991; Watanuki, 1992; Hario, 1994; Yorio *et al.*, 1996; Bukaciński *et al.*, 1998; Schmutz & Hobson, 1998; Gaston *et al.*, 2009). Adult birds are also taken by larger gull species. Great Black-backed Gulls (*L. marinus*), for example, eat substantial numbers of adult seabirds that breed at colonies close to their nest sites (Harris, 1965). Gulls are known to hunt mammals, including rabbits and moles (Tinbergen, 1953; personal observations). They also eat fish, which they catch through dip and plunge diving and surface skimming, both alone and in flocks (Tinbergen, 1953; Brown *et al.*, 1967; Hunt & Hunt, 1976b; Isenmann, 1976; Witt *et al.*, 1981; Götmark *et al.*, 1986; Götmark, 1987; Håstad *et al.*, 2005), while foot paddling may be used to locate fish eggs (Moyle, 1966). Terrestrial, freshwater and marine invertebrates also contribute to the natural gull diet (Tinbergen, 1953; Hailman, 1964; Snow & Snow, 1968; Harris, 1970; Spaans, 1971; Vernon, 1972; Isenmann, 1976; Jarvis & Southern, 1976; Trapp, 1979; Witt *et al.*, 1981; Sibly & McCleery, 1983a; Götmark, 1984; Curtis *et al.*, 1985; Welham, 1987; Ambrose, 1986; Irons *et al.*, 1986; Nogales *et al.*, 1995; Goutner, 1994; Schmutz & Hobson, 1998; Kubetzki *et al.*, 1999; Silva *et al.*, 2001; Kubetzki & Garthe, 2003; Kim & Monaghan, 2006; Coulson & Coulson, 2008b; Mills *et al.*, 2008). Fast moving prey, such as crabs or flying insects, are caught through terrestrial or aerial pursuit (Tinbergen, 1953; Vernon, 1972; Kirkham & Morris, 1979; Mudge & Ferns, 1982; Welham, 1987; Delhey *et al.*, 2001), while slower prey are seized from the ground, sometimes in a dive (Isenmann, 1976; Curtis *et al.*, 1985; Delhey *et al.*, 2001), or revealed by foot paddling (Tinbergen, 1953; Vernon, 1972; Curtis *et al.*, 1985). Stationary prey, for example limpets, are prised off their substrate with the bill (Favero *et al.*, 1997), while hard or large prey items, like clams, cockles or large fish, are broken up by hammering them against the ground or dropping them from a height over a hard surface (Tinbergen, 1953; Trapp, 1979; Irons *et al.*, 1986). Although the majority of gulls' food intake is derived through carnivory, these birds also consume vegetable matter, including grain, fruit and algae (Threlfall, 1968; Vernon, 1972; Witt *et al.*, 1981; Götmark, 1984; Murphy *et al.*, 1984; Goutner, 1994; Nogales *et al.*, 1995; Favero & Silva, 1998; Kubetzki *et al.*, 1999; Ludynia *et al.*, 2005; Kim & Monaghan, 2006). Inorganic substances, such as stones, are also eaten to help break down solid food in the gizzard (Goutner, 1994).

5.1.2 Locating food

In common with many birds, gulls rely heavily on acute visual abilities for food finding (Frings *et al.*, 1955). Gulls have tetrachromatic vision, with the maximum sensitivity of one of their photoreceptors, the SWS1 cone, in the ultraviolet (UV) range of the electromagnetic spectrum (Ödeen & Håstad, 2003). The latter is thought to be an adaptation to terrestrial foraging and other omnivorous activities rather than to fishing at sea, as the SWS1 cone of the closely related piscivorous terns, along with species from other families specializing in marine dip-and-plunge diving, has a maximum sensitivity at longer wavelengths, in the violet part of the spectrum (Håstad *et al.*, 2005). Most gulls forage diurnally, although certain species, including the Ring-billed Gull, Grey Gull (*Leucophaeus modestus*) and Swallow-tailed Gull (*Creagrus furcatus*) also find food nocturnally (Hailman, 1964; Kirkham & Morris, 1979; Emond *et al.*, 2006) and thus have retinal adaptations to allow them to cope with low light intensities (Emond *et al.*, 2006). Nocturnal species may also use tactile stimulation to find food at night (Emond *et al.*, 2006), probing wet sand and mud with their bills to detect movement, in a manner reminiscent of the foraging strategy of other shorebirds (Piersma *et al.*, 1998).

Gulls are thought to use social cues for locating food. At colonies and communal roosts, individuals sometimes follow each other to food sources (Evans, 1982a). Such behaviour may or may not be compatible with the "information centre" hypothesis of food-finding (Andersson *et al.*, 1981; Evans, 1982a), which suggests that birds assemble in colonies and at roosts primarily so that they can exploit food sources more efficiently than they could alone (Ward & Zahavi, 1973). Gulls are, however, attracted by the sight of another individual feeding and congregate in that area (Andersson *et al.*, 1981). They are also known to emit calls when they depart for foraging trips and come across food (Frings *et al.*, 1955; Evans, 1982a), which may aurally attract conspecifics (Frings *et al.*, 1955; Evans, 1982a), and might be advantageous to the callers since flock feeding can be a more successful way of finding food than solitary foraging (Götmak *et al.*, 1986; but see Willson & Marston, 2002).

Another sense that might be employed by foraging gulls is smell. Olfactory cues are used widely by procellariiform seabirds as a means of locating food (Grubb, 1972; Verheyden & Jouventin, 1994; Nevitt, 2000; Nevitt *et al.*, 1995; 2004). These sensory abilities develop early, with chicks able to detect the compounds employed in food finding (Cunningham *et al.*, 2003). The same molecules are also recognized by other seabirds (Cunningham *et al.*, 2008), and olfaction has been found to play a role in foraging in several other avian families, including the galliforms, and passeriforms (for a review, see Roper, 1999; Mennerat *et al.*, 2005). Although in folklore gulls are said to have a sense of smell (Frings *et al.*, 1955), scientific reports are mixed about the importance of olfaction in these species. Their olfactory bulb is approximately the same size as that of chickens (*Gallus gallus domesticus*) (Bang & Cobb, 1968), which are known to respond to olfactory cues in feeding (Rowe & Guilford, 1996; Marples & Roper, 1996; Roper & Marples, 1997). Moreover, the use of olfaction in a different context, courtship, has been found in the Crested Auklet (*Aethia cristatella*), which is a member of the same sub-order as the gulls (Thomas *et al.*, 2004; Baker *et al.*, 2007). However, gulls did not find odorous food in experiments where it was concealed (Frings *et al.*, 1955), although the logic linking this result to an absence of olfactory ability is weak (Roper, 1999). Gulls also did not respond to sponges soaked in a prey-related odour whereas procellariiform birds did (Grubb, 1972; Lequette *et al.*, 1989), but again, evidence is lacking to completely rule out the role of smell in foraging gulls.

5.1.3 Acquiring foraging practices

The diversity of foraging methods and habitats seen in gulls sets them apart from many other seabirds and shorebirds, including other charadriiform birds (Pierotti & Annett, 1990), which tend to feed mostly on aquatic or intertidal organisms (Burger, 1987; Furness & Monaghan, 1987). However, such wide foraging expertise takes time to perfect, and is acquired during the first years of an individual's life. Compared to adults, young gulls spend more time searching for food (Verbeek, 1977b; Burger & Gochfeld, 1981b; MacLean, 1986), have longer intervals between feeds (Burger & Gochfeld, 1983; Burger, 1987), have lower feeding rates (Greig *et al.*, 1983; Skórka & Wójcik, 2008), consume a smaller proportion of food that is handled (Greig *et al.*, 1983; Bertellotti & Yorio, 2000), drop food more frequently (Verbeek, 1977c; Burger & Gochfeld, 1981b; Bertellotti & Yorio, 2000), swallow more inedible substances (Verbeek, 1977c), initiate a greater number of kleptoparasitic interactions (Verbeek, 1977b; 1977c; Greig *et al.*, 1983; Bertellotti & Yorio, 2000; Skórka & Wójcik, 2008) and are more likely to drop hard food items over surfaces that do not to break them (Ingólfsson & Estrella, 1978; Drexler Rockwell, 1982). Juvenile gulls are also more likely to consume food that is easier to capture, handle and locate (Burger & Gochfeld, 1983; Copello & Favero, 2001), and are less able and inclined to execute difficult foraging techniques, such as surface plunge diving and digging (Verbeek, 1977b; 1977c; Searcy, 1978; Copello & Favero, 2001; Willson & Marston, 2002). They also frequently feed in suboptimal areas (Moyle, 1966; Davis, 1975b; Monaghan, 1980). Similar trends are found amongst the terns (Dunn, 1972; Buckley & Buckley, 1974).

Young gulls practice the motor skills needed in foraging. Juvenile Herring Gulls (*L. argentatus*) use play to rehearse drop-catches, where an item is released from a height and caught before it hits the ground, with non-food objects (Gamble & Cristol, 2002). Foraging is also learned via trial and error, with marked improvements in particular feeding methods recorded over the juvenile and sub-adult periods in many species (Verbeek, 1977b; Ingólfsson & Estrella, 1978; MacLean, 1986; Skórka & Wójcik, 2008). Social learning through observation by young of the foraging techniques of adults (Ingólfsson & Estrella, 1978; Greig *et al.*, 1983; Annett & Pierotti, 1999) and vertical transmission of feeding practices from parents to offspring (Annett & Pierotti, 1999) may also occur. In terns, adults tutor juveniles in fish capture skills by demonstrating the necessary manoeuvres while the juveniles imitate them (LeCroy, 1972). The time required to learn how to feed effectively and efficiently has been cited as one reason why gulls' maturity is delayed, so that many species do not breed until they are at least four years old (Spaans, 1971; Chabrzyk & Coulson, 1976; Coulson *et al.*, 1982; Greig *et al.*, 1983; MacLean, 1986).[39]

5.1.4 Pre-fledging foraging behaviour

Gull chicks rely entirely on their parents for food provisioning (Starck & Ricklefs, 1998), and do not feed wholly independently until several weeks after fledging (Burger, 1981; Spear *et al.*, 1986). There is little information on the mechanisms controlling how chicks at this stage begin to acquire independent feeding practices. It is known that some types of foraging behaviour emerge before fledging. Attempted kleptoparasitism, for example, has been recorded in three-week-old Ring-billed Gulls (*L. delawarensis*), apparently induced by lack of adequate nourishment from the parents (Elston & Southern, 1983).

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[39] Delayed maturity and accompanying age-related differences in foraging ability is also found in other seabird species, including pelicans, frigatebirds and cormorants (Furness & Monaghan, 1987).

The innate pecking preferences of chicks are better understood, however. Immediately post-hatching chicks peck at objects of particular shapes and colours (see Chapters 3 and 4). Aspects of this pecking behaviour are intimately connected to the feeding process, as newly hatched chicks aim pecks at their parents' bills without induction or prior experience, in order to bring about food regurgitation, in a behavioural process known as the pecking response (section 3.1.1). This behaviour has been extensively studied, with most work using models of the parental bill, and modifications thereof, as a starting point for exploring the release of pecking during food begging (e.g. Tinbergen & Perdeck, 1950; Hailman, 1967; Margolis *et al.*, 1987; Alessandro *et al.*, 1989; ten Cate *et al.*, 2009). Far fewer studies have investigated the nature and role of innate feeding preferences in gull chicks.

In one such study, American Herring Gull (*L. smithsonianus*) chicks that had been hand-raised on cat food were fed various cuts of fish from the age of 25 days. All chicks swallowed the fish head first, and appeared to attend to the width of the head end relative to that of the tail in orienting their food, rather than to particular features such as the eyes or fins (Hunt & Smith, 1964). In another study, laboratory hatched American Herring Gull and Ring-billed Gull chicks were reared on earthworms, pink cat food or green cat food for five days. On the sixth day food preferences were tested in a series of choices between two of these food types. Although the training food was preferred in the vast majority of tests where this substance was provided, worms were selected by most chicks given the choice of two unfamiliar food substances. The pink cat food was the next most popular choice in this test, although some chicks did not respond to either of the food substances presented (Rabinowitch, 1968).

The latter study indicates a mechanism by which gulls can become conditioned to particular foodstuffs. Although dietary generalists at the family and species level, many individual gulls show specializations in their foraging behaviour (Harris, 1965; Davis, 1975b; Sibly & McCleery, 1983b; McCleery & Sibly, 1986; Pierotti & Annett, 1987; 1991; Watanuki, 1992).

There are indications that such behaviour crystallises over the sub-adult period, with juveniles showing a significant degree of plasticity in their feeding choices that declines as they mature (Davis, 1975b). In prey selection experiments, adults prefer prey of the size they commonly encounter in their foraging habitat, suggesting that they form specific search images of food through experience (Irons *et al.*, 1986). Such specializations could also be related to other influences on an individual's diet, for example constraints imposed on foraging habits as a result of sex, age or interspecific competition (Moyle, 1966; Verbeek, 1977b; Monaghan, 1980; Niebuhr, 1983; Greig *et al.*, 1985; 1986; Delhey *et al.*, 2001).

The results of Rabinowitch's (1968) study also suggest an innate preference for consuming worms, which overrides any specialization which may occur through training on other food substances. This is noteworthy considering that in many gull species, a higher proportion of worms and similar prey are selected by parents foraging for their chicks, compared to levels found in the diet at other times of a gull's life (Nogales *et al.*, 1995; Stanworth, 1998). This trend is particularly pronounced in the first week after hatching (section 5.1.5), after which the diet delivered to chicks becomes ever more similar to that normally consumed by adults (Nogales *et al.*, 1995; Stanworth, 1998). This indicates that certain properties of the food substances chosen for young chicks are required at this early stage of life (Annett & Pierotti, 1989; Nogales *et al.*, 1995).

5.1.5 Dietary switches in chick feeding

Chicks of most species are reared on a diet that differs from that of adults. Typically, chicks are reared on food that is rich in amino acids, necessary for growth and development (O'Connor, 1984; Ricklefs *et al.*, 1998). For many species, this means chicks consume a higher proportion of food from animal sources than adults, although in some birds, including pigeons and certain seabirds, chicks' protein needs are met through the delivery of special crop secretions by the parents (O'Connor, 1984). In addition to protein and energy, growing chicks often require specific nutrients, such as calcium for skeletal growth (Pierotti & Annett, 1987; Beintema *et al.*, 1997; Schew & Ricklefs, 1998), and can only eat food that is small and easy to swallow and digest (Nogales *et al.*, 1995; Lehikoinen, 2005). These demands are also addressed through dietary switches and parental secretions (Schew & Ricklefs, 1998).

In gulls, deviations in the diet of chicks from that typical of adults, and the gradual convergence of the two as chicks age, have been recorded in many species, including Western Gulls (*L. occidentalis*) (Annett & Pierotti, 1989), Herring Gulls (Nogales *et al.*, 1995; Bukacińska *et al.*, 1996), Yellow-legged Gulls (*L. michahellis*) (Duhem *et al.*, 2005; Ramos *et al.*, 2009), American Herring Gulls (Belant *et al.*, 1993), Kelp Gulls (*L. dominicanus*) (Favero & Silva, 1998; Bertellotti & Yorio, 1999; Silva *et al.*, 2001), Ring-billed Gulls (Kirkham & Morris, 1979), Lesser Black-backed Gulls (Stanworth, 1998), Glaucous-winged Gulls (*L. glaucescens*) (Irons *et al.*, 1986) and Audouin's Gulls (*Ichthyaetus audouinii*) (Pedrocchi *et al.*, 1996) (Table 5.2). This phenomenon can also be inferred in other species, such as the Common Gull (*L. canus*) (Kubetzki *et al.*, 1999), through changes in the adult diet during the breeding season, which closely parallels that of the chicks for which they are providing (Welham, 1987; Brown & Ewins, 1996).

Reports on the direction of these dietary switches are often conflicting, even within a single species. Adult Kelp Gulls in the Antarctic Peninsula, for example, have been shown to consume a diet rich in limpets, while that of young chicks is predominantly krill (Silva *et al.*, 2001). A study of the same species in Patagonia, however, showed a switch away from the adult diet of marine invertebrates, to a regime comprising of mainly fish in chicks (Bertellotti & Yorio, 1999). Such discrepancies could be partly due to variations in food availability over a species' range, but could also be an artefact of the different methods employed to assess diet (Brown & Ewins, 1996). Several techniques are used for seabird diet studies, including examination of material expelled as regurgitated pellets or faeces (e.g. Bukacińska *et al.*, 1996; Nogales *et al.*, 1995), analysis of spontaneous (Belant *et al.*, 1993; Ramos *et al.*, 2009) or forced regurgitations (e.g. Hunt, 1972; Duhem *et al.*, 2005), dissection of stomach contents (e.g. Spaans, 1971; Welham, 1987) and direct observations of feeding (Kirkham & Morris, 1979; Trapp, 1979). Each of these methods has its shortcomings (Barrett, *et al.*, 2007). Pellets, for example, are biased towards the preservation of undigested material, such as vegetation, while under representing easily digested soft-bodied prey (Brown & Ewins, 1996; Barrett *et al.*, 2007, but see Spaans, 1971; Annett & Pierotti, 1989).[40] In the Kelp Gull studies cited above, both used pellet analysis, but Silva *et al.* (2001) examined regurgitates as well. However, despite such potential shortcomings, it is possible to pick out some overall trends in the differences between adult and chick diets from the various published accounts of this phenomenon (Table 5.2).

One of the most consistently reported results comes from diet studies of gulls nesting in the vicinity of urban areas, which show an increase in food from natural sources, namely fish and invertebrates, and a concurrent decrease in food from landfill, during the early chick period (Götmark, 1984; Annett & Pierotti, 1989; Belant *et al.*, 1993; Smith & Carlile, 1993; Hillström *et al.*, 1994; Stanworth, 1998; Ludynia *et al.*, 2005). Other apparent trends include a shift towards small (e.g. Annett & Pierotti, 1989; Ramos *et al.*, 2009), and soft prey in the chick diet (e.g. Kirkham & Morris, 1979; Nogales *et al.*, 1995). The predominance of fish and worms in the chick diet has also been reported in studies of chick provisioning without direct comparison to diets at other ages (e.g. Brown & Ewins (1996) in a study of Ring-billed Gulls).

5.1.6 Explaining the dietary switch

The mechanisms behind the initiation of the observed dietary switches are not certain. Studies in Western Gulls and American Herring gulls show that the switch is proximately caused by the sudden appearance of (hatching)

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[40] Little work to date has examined gull diets using more modern techniques (Barrett *et al.*, 2007), such as stable isotope analysis (e.g. Knoff *et al.*, 2002) or fatty acid signatures (e.g. Kakela *et al.*, 2009), and only one such study has addressed the differences between chick and adult diets (Schmutz & Hobson, 1998).

chicks, such that neighbouring gulls consume different diets if they are at varying stages of the reproductive cycle (Annett, 1987; Pierotti & Annett, 1987; Annett & Pierotti, 1989). However, this finding does not reveal why chick hatching should modify parental behaviour in this fashion. One possible explanation is that, in common with patterns found in other species, these changes are necessary in order to meet chicks' early nutritional and energetic needs (Spaans, 1971; Kirkham & Morris, 1979; Annett & Pierotti, 1989; Nogales *et al.*, 1995).

Of the foods switched to during the early chick phase (Table 5.2), fish in particular are a good source of energy, protein and lipids (Hunt, 1972; Pierotti & Annett, 1987; Annett & Pierotti, 1989), and are easy to digest (Nogales *et al.*, 1995), with few hard parts, hence maximising the parents' energetic return per foraging trip (Bertellotti & Yorio, 1999). Indeed, even the bones of fish can be broken down and assimilated by chicks in their first week or life, forming a useful supply of calcium for skeletal growth (Spaans, 1971). Seabird chicks too, have a high energy and nutritive content, increasing the growth rate and fledging success of gull chicks consuming them relative to chicks fed lower quality foodstuffs (Watanuki, 1992; Bukacińska *et al.*, 1996). Similarly, insects contain ample protein (Kirkham & Morris, 1979), and, along with worms, are easy to digest, especially in the larval stages (Kirkham & Morris, 1979; Nogales *et al.*, 1995).[41] It is also thought that fish and worms might provide young chicks with essential vitamins and minerals necessary for growth (Nogales *et al.*, 1995). Evidence that both fish and invertebrates are equally appropriate food for chicks comes from a study of Black Terns (*Chlidonias niger*), in which growth and survival did not differ in chicks fed either a primarily piscivorous or insectivorous diet (Gilbert & Servello, 2005, but see Beintema *et al.*, 1997).

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[41] Studies of earthworms and other terrestrial invertebrates that are regularly consumed by certain human populations have revealed the high protein, lipid, energy, vitamin and mineral content of these foodstuffs (Paoletti *et al.*, 2000; 2003; Marconi *et al.*, 2002).

Perhaps unsurprisingly, the foods that parents switch away from when caring for young chicks do not share such beneficial properties. Refuse at landfill, for example, may have a high caloric value but low nutritive quality, containing a large proportion of fat, but smaller amounts of protein, vitamins and minerals, and marked quantities of indigestible material (Hunt, 1972; Pierotti & Annett, 1987). Other foods that are switched away from, such as molluscs, are low in energy and nutrients, as well as having a high percentage of indigestible matter in the form of shell (Spaans, 1971; Niebuhr, 1983; Murphy *et al.*, 1984; Pierotti & Annett, 1990; 1991).

The diet of young chicks could also be determined by their ability to physically handle and swallow food (Annett & Pierotti, 1989; Kirkham & Morris, 1989; Hillström *et al.*, 1994). Small chicks are sometimes seen to reject food (Spaans, 1971; Pierotti & Annett, 1987; Pedrocchi *et al.*, 1996; Stanworth, 1998), which their parents may respond to by breaking it up or reswallowing it, before regurgitating it again some minutes later. This probably serves to increase the manageability of the food for the chicks, by further softening and perhaps digesting it along with producing smaller pieces (Spaans, 1971; Kirkham & Morris, 1979; Mudge & Ferns, 1982; Pedrocchi *et al.*, 1996).[42] Furthermore, chicks' gapes grow faster relative to the rest of their skeleton in early life, indicating that food consumption may be constrained by gape size in the period succeeding hatching (Stanworth, 1998). The small and soft nature of the prey typically switched to by parents while feeding young chicks is likely to facilitate food handling (Kirkham & Morris, 1979; Annett & Pierotti, 1989). In addition to ensuring that chicks can feed successfully, delivering appropriately sized and textured prey also speeds up the whole feeding process, helping to reduce the likelihood of kleptoparasitism, which places small chicks at risk both through the loss of food and the threat of cannibalism (Annett & Pierotti, 1989; Hillström *et al.*, 1994).

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[42] Food for chicks is also sometimes reswallowed by the feeding parent to prevent theft by neighbouring birds in the colony (Butler & Trivelpiece, 1981).

Dietary switches could also be brought about by extrinsic factors, such as prey location. During early chick rearing, adults take turns to depart on foraging trips and attend to the chicks (Spaans, 1971; Morris, 1987; Bukacińska *et al.*, 1996). It is vital that such parental care is well coordinated, to minimize the risk of brood loss through starvation or predation (Morris, 1987; Bukacińska *et al.*, 1996). Thus, an adult's usual foraging rhythm is disrupted, such that certain feeding grounds normally visited outside the breeding season, for example the intertidal zone, are not always accessible at times when food is required by chicks (Spaans, 1971). This could result in skews in the type of prey observed in chick meals. Similarly, access to distant feeding grounds might be constrained by the time taken to make the round trip (Hunt, 1972; Bukacińska *et al.*, 1996; Pedrocchi *et al.*, 1996), or changes in the diet might be a result of intense competition for top quality food at normal feeding grounds during the breeding season (Smith & Carlile, 1993; Bukacińska *et al.*, 1996). Alternatively, seasonal abundance of certain prey types could also account for their use as food items for young chicks (Spaans, 1971; Kirkham & Morris, 1979; Belant *et al.*, 1993; Bertellotti & Yorio, 1999; Kubetzki *et al.*, 1999), although studies have shown that dietary switches are not synchronized with seasonal prey changes (Pierotti & Annett, 1987; Annett & Pierotti, 1989). Conversely, absences of dietary switches away from nutritionally or physically suboptimal foods, such as refuse, may occur because the gulls concerned do not have alternative food sources available (Duhem, *et al.*, 2005).

Dietary switches do appear to be adaptive, however, suggesting that although they might be influenced by extraneous properties of the birds' environment, factors intrinsic to gulls are at least partly responsible for their occurrence. In Western Gulls, breeding pairs have different feeding strategies during the breeding season. The majority of those that never provide natural prey for their chicks breed for only one season and do not fledge many young, while pairs that take a substantial proportion of fish produce a large number of eggs, and have high hatching and fledging success over many seasons (Annett & Pierotti, 1999). Similarly, Herring Gulls that fail to make the dietary switch during the first ten days of their chicks' lives have a lower fledging success than those that do (Bukacińska *et al.*, 1996), while Glaucous-winged Gulls (*L. glaucescens*) which feed their chicks on mussels instead of fish suffer poor reproductive success (Murphy *et al.*, 1984). Even if chicks do survive to adulthood, the food brought to them in early life can have profound effects on their fitness (Kitaysky *et al.*, 2006).

5.1.7 Dietary switches and innate feeding preferences

If the dietary differences between gulls during early life and adulthood are governed by the nutritional, energetic or physical requirements of the chick, this could have led to selection pressure on chicks' innate feeding preferences, such that they are adapted to peck at objects resembling the food items they require from hatching (so as to consume such items first, before their siblings), namely fish, worms and insects.[43] Fish often have pale to white flesh and scaly, silvery skin, while worms are typically segmented, and red to brown in colour. Insect larvae are also often white to brownish and striped or segmented. All these food classes are elongated in shape.

Such foods have some resemblance to the superstimulus (SS), a long, thin, red object with three terminal white stripes, towards which young chicks have been found to exhibit a supernormal pecking response (Tinbergen & Perdeck, 1950). Although it has been suggested that supernormal pecking is an adaptation to the angle at which chicks first view their parents' bills (Tinbergen & Perdeck, 1950), or simply not adaptive at all (Ramachandran, 2004), this behaviour could reflect innate feeding preferences (section 4.1.3). The extra level of attractiveness brought about by food should such supernormal properties exist could also help explain how chicks switch their attention from pecking at their parents' bills, to pecking at food items. Other

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[43] Innate preferences could have arisen even if the food provided by parents does not address chicks' needs, as any adaptation that would have enhanced chicks' likelihood of efficiently consuming food in the face of sibling competition could would confer a selective advantage, and thus become fixed in the population.

possible cues for focussing chicks on food include smell and parental behaviour.

5.2 EXPERIMENTAL QUESTIONS

The experiments carried out in this chapter were designed to address two separate lines of enquiry about how chicks switch their attention from pecking their parents' bills to eating, and whether innate feeding preferences exist:

1) Does olfaction play any role in food recognition in gull chicks?
2) Do objects protruding from the parent's bill tip draw chicks' pecks away from the gonys spot?
3) Given a choice of plain or striped food items, which do chicks peck at and which do they eat?
4) What size and shape of food do chicks prefer, and which can they consume?

5.3 METHODS

Fieldwork was carried out during three consecutive breeding seasons from 2007 to 2009 on Flat Holm, where Lesser Black-backed Gulls (*Larus fuscus*) were studied (section 2.2.1). As seen on Flat Holm, where Herring and Great Black-backed Gulls also nest (section 2.2.1), Lesser Black-backed Gulls frequently breed sympatrically with other gulls (Harris, 1964; Brown, 1967a; 1967b; Hunt & Hunt, 1973b; Sobey, 1976; Kim & Monaghan, 2006), a coexistence that is partly maintained by differences in their feeding ecology (Hunt & Hunt, 1973b). Compared to the similarly proportioned Herring Gull, Lesser Black-backed Gulls tend to take more marine food (Brown, 1967a; Hunt & Hunt, 1973b; Kubetski & Garthe, 2003; Kim & Monaghan, 2006). In common with many other gulls, Lesser Black-backs forage at landfill sites, although again their manner of feeding is slightly different to Herring Gulls, with digging not found in Lesser Black-backed Gulls (Verbeek, 1977a). The year round availability of food at landfills and other anthropogenic food sources is thought to have brought about changes in the wintering behaviour of this species. Traditionally, Lesser Black-backed Gulls migrated south to winter primarily in the Iberian Peninsula and North-West Africa, but in recent decades individuals have begun to stay in the UK (Brown, 1967a; Baker, 1980). Little work has been carried out on the feeding ecology of chicks, although it is known from supplementary feeding experiments that the amount of food delivered by parents in early life has significant effects on chick growth and survival to fledging (Bukaciński *et al.*, 1998).

In 2007 and 2008, methods of chick selection and care were as described in sections 2.3.1 and 2.3.2. In 2009, chicks were removed from the nest after hatching, as in 2006 (see section 3.3.1.1), although they were kept in the former fog horn keeper's cottage instead of the Victorian barracks, and were housed together both before and after behavioural tests. Unless otherwise specified, the protocol used for presenting chicks with stimuli in behavioural tests was the same as that detailed in section 3.3.2.1. Work took place with permission from the Countryside Council for Wales, under licences OTH:SB:02:2007/2008/2009, while experiments conformed to the guidelines on the ethical treatment of animals in behavioural research, set by the Association for the Study of Animal Behaviour.

Experiment 5.1 - Testing the possible role of olfaction in chick feeding

Chicks' olfactory capabilities were assessed using a technique adapted from that described by Porter *et al.* (1999) for domestic chicks (*Gallus gallus domesticus*), which has subsequently been successfully employed with other seabird species (Cunningham *et al.*, 2003; Bonadonna *et al.*, 2006).[44] Each

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[44] It is hard to see how experiment 5.1 relates to a situation in which chicks in the wild would use olfaction (if indeed they are able to smell). However, the technique was thought to be quick and easy, and thus a starting point on which to base other experiments on olfaction. Moreover, the researchers who successfully employed this method with the chicks of other

chick was wrapped in a bird bag and held on its back, with the head pointing slightly downwards, under a 100 W infrared heat lamp (Exo-Terra Heat Glo), such that the chick's body threw a shadow over its eyes (Fig. 5.1). After a short period of time (usually approximately 20 seconds), some chicks entered a sleep like state, and were presented with four odour stimuli in a random order.

Fig. 5.1. A Lesser Black-backed Gull chick in a sleep-like state under a 100 W infrared heat lamp in experiment 5.1, testing olfactory capabilities (after Porter *et al.* 1999).

In 2007, the odour sources were 20 g of tuna in 100 ml of sunflower oil, 20 g of freshly mashed tiger worms (*Eisenia foetida*) in 100 ml of sunflower oil, 100 ml of sunflower oil alone and 100 ml of distilled water. Tuna and *E. foetida* were chosen because they were thought to be prey items of biological significance to the gull chicks since parents often bring worms and fish to their offspring (e.g. Annett & Pierotti, 1989; Brown & Ewins, 1996).

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seabird species, made inferences to the use to olfaction in a natural setting from their findings (Cunningham *et al.*, 2003; Bonadonna *et al.*, 2006).

Sunflower oil was used as a relatively odourless carrier of scents (although the sunflower oil treatment alone was designed to test whether chicks did respond to its smell), and distilled water acted as the overall control.

In 2008, chicks were tested with odours that have been found to be associated with feeding in other seabird species. These were 100 ml of cod liver oil (Grubb, 1972; Lequette, 1989), 200 mmol l^{-1} 2-methyl pyrazine (Nevitt *et al.*, 2004), and both 1.0 µmol l^{-1} and 0.1 µmol l^{-1} dimethyl sulphide (DMS) (Cunningham *et al.*, 2003; Bonadonna *et al.*, 2006). Both the pyrazine and DMS are released by decomposing krill (Nevitt *et al.*, 2004), which is consumed by gulls (Mills, 2008; Tomita *et al.*, 2009) and fed to their chicks (Favero & Silva, 1998). The concentrations of pyrazine and DMS were chosen because they have been successfully detected by seabirds and their chicks in other studies (Cunningham *et al.*, 2003; 2008; Nevitt *et al.*, 2004). The pyrazine and DMS were purchased from Sigma-Aldrich (UK) and made up to the relevant concentrations in a laboratory in Cardiff University before being transported to Flat Holm in sealed glass laboratory bottles.

The appropriate quantities of all odorants were transferred to squeezable plastic bottles immediately prior to the start of the experiment. The bottles were then squeezed gently and their nozzles passed in front of the chicks' bills at a distance of approximately 2 cm for ten seconds. After Porter *et al.* (1999), the reactions of the chicks were scored as follows:

0 = no observable response to the stimulus
1 = minimal response (beak clapping and/or slight head movement)
2 = distinct head shaking (lateral and up/down)
3 = abrupt jerking of the head (more rapid than 2); may be accompanied by shrill peeps

Discretion was used in applying these criteria, as the chicks were frequently found to whistle softly even when apparently asleep. Each chick was used only once, and returned to the holding box after the trial. The odour detection tests were successfully carried out on 23 incubator-hatched chicks on three separate dates in May and June 2007. In 2008, incubator-hatched chicks were tested on 5th and 6th June, but on neither date did sufficient number of chicks "sleep" to achieve an adequate sample size for statistical tests (22 chicks were tested, of which five responded partially, and two fully, to the experimental set-up).

Experiment 5.2 - Diverting chick pecking from the gonys spot

This experiment was similar to those detailed in sections 3.3.2 and 4.3, using model heads to test the pecking response of chicks. In this experiment, however, an object was attached to each model's bill tip to test whether hatchlings still directed their pecks preferentially to the gonys spot in this situation. Under natural conditions, such an object could be food. A range of different shapes was used to test if some were better at redirecting the attention of chicks away from the gonys spot than others.

This experiment was successfully carried out on 27 naïve (incubator-hatched) chicks on four dates between 10th and 14th June 2008. All chicks were between 6.0 and 48.3 hours old at the time the experiment commenced, with a mean age of 28.4 hours. Chicks' reactions to six different stimuli were tested. The Control was a two-dimensional stick-mounted card model of an adult Lesser Black-backed Gull's head in profile as described in experiment 3.1. Four of the five other stimuli were identical to the Control except for the addition of a particular shape (Square, Circle, Star or Stick) at the end of the bill tips (Fig. 5.2). All these shapes were of equal area (64 mm^2). Chicks were also presented with a 3 mm diameter SS (stripe width = 2 mm, stripe separation = 2 mm, distance from tip to first stripe = 16 mm). The same precautions were taken to avoid pseudoreplication as described in experiment 4.1.

Fig. 5.2 Examples of the stimuli used in experiment 5.2. Top to bottom: Star, Stick, Square, Circle, Control, SS.

Experiment 5.3 - Assessing chicks' choices of plain or striped food items

5.3a Binary food choices

These experiments were successfully carried out with over 60 chicks of unknown age and experience (removed from the colony post-hatching) on six consecutive dates from 24th to 29th May 2009. Chicks were given a choice of two different food items of 25 mm length and 5 mm width, attached to a two-pronged fork such that they were spaced by 22 mm (Fig. 5.3). The choices of food were:

- Plain chicken breast, or chicken breast striped with red cochineal food colouring (stripes approximately 2 mm thick, separated by 2 mm).
- Plain cooked pasta, or ridged ("segmented") pasta.
- Plain chicken breast, or a length of freshly killed earthworm (*E. foetida*).

Fig. 5.3 A chick with a binary choice of earthworm or chicken in experiment 5.3a.

Every chick was presented with each choice once during the course of the experiment. The order of the trials was randomized, as was the position of the food item (whether it was on the left or right prong of the fork). Between trials, all chicks were replaced in the holding box with the other chicks, such that they were given a break of approximately 15 minutes between each presentation to minimize habituation to the experimental process.

Chicks made their choices in an arena identical to that described in section 3.3.2.1. Each chick was placed in the arena for approximately one minute before the start of the trial, after which the fork was slowly introduced and placed approximately 2 cm from the chick's beak, with each stimulus equidistant from the side of the bill. A Control head was also placed in the arena in front of the stimulus to help elicit pecks. Twelve different heads were available (six right view, six left view), the presentation of which was randomized for each trial to avoid pseudoreplication of stimuli (Ruxton & Colegrave, 2006). Several different food stimuli were also available for each trial to attempt to eliminate this problem. The first and second pecks each chick made were recorded. Chicks were prevented from eating the stimuli.

5.3b Choice of four stimuli

This experiment was successfully carried out with 62 chicks (of a possible 63) on six consecutive dates from 24th to 29th May 2009. All chicks were taken from their parents post-hatching and were thus of unknown age and experience. Chicks were presented with four different sizes of chicken breast on a four pronged fork, again introduced to the arena along with a Control head. The smallest piece of meat was 2.5 mm x 25 mm, the second smallest was 5 mm x 30 mm, the second largest was 10 mm x 40 mm, and the largest was 15 mm x 50 mm. The mean distance between each piece of chicken was 22 mm (Fig. 5.4). The position of each size of meat on the stimulus was randomized and several different pieces of meat of each size were used during the course of the experiment to minimize pseudoreplication of stimuli (Ruxton & Colegrave, 2006). The experimental set-up was the same as that described in experiment 5.3a. The chicks used were the same as those in experiment 5.3a, and this trial was therefore placed with the three binary choice experiments in the randomization of experimental order for each chick.

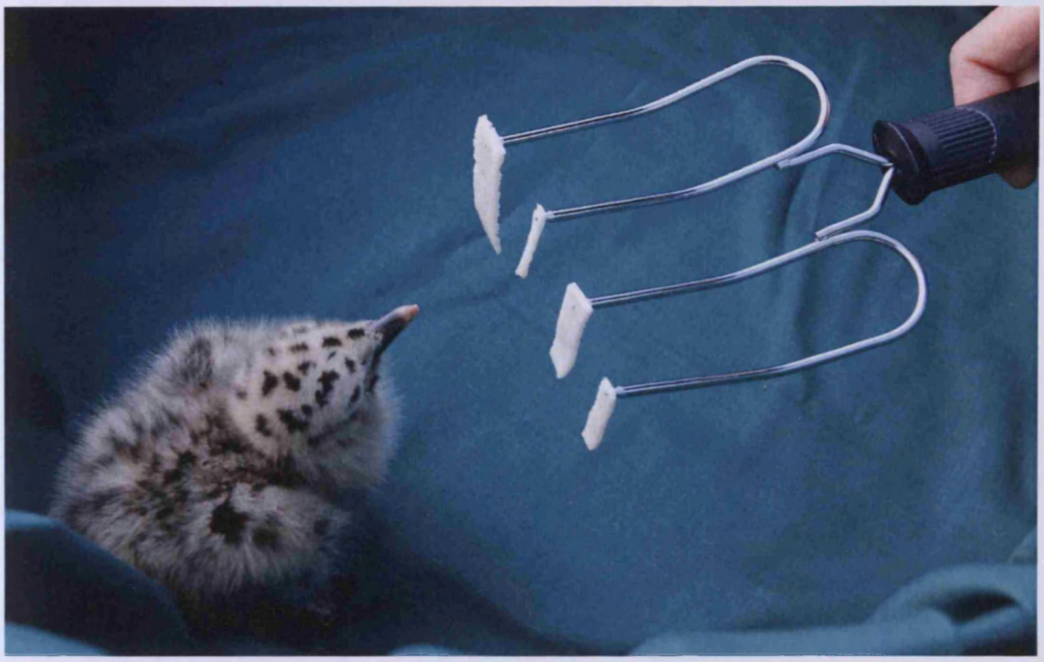


Fig. 5.4 A chick facing a choice of four food stimuli in experiment 5.3b.

5.3c Pecking and eating choices of several different food items

This experiment was carried out with the chicks used in experiments 5.3a and 5.3b, but always after these experiments had been completed. These chicks were thus of unknown age and experience, having been removed from the parental nest post-hatching. The experiment was successfully undertaken with 64 individuals (of a possible 65 chicks tested) on six consecutive dates between 24th and 29th May 2009. Chicks were placed individually in the arena, in the centre of which was positioned an area of brown woven sacking. On the sacking were six pieces of round chicken breast (Discs) (diameter = 11.5 mm), six pieces of rectangular chicken breast (Strips) (25 mm x 3 mm) and six lengths of freshly killed earthworms (Worms) (*E. foetida*) (25 mm x 2-3 mm). All three classes of food were designed to be of approximately the same area. The Discs were further designed to be approximately the same size as the gonys spot on an adult Lesser Black-backed Gull's bill. If necessary, chicks' attention was drawn to the food items with a model adult Control head. The first six pecks chicks made to the food items were recorded. If chicks ate any food items during these six pecks, these were recorded too, but the food was not replaced. Consecutive pecks to the same food item were recorded as one peck only, but if a chick pecked first at a particular food item, then pecked at a different one, before returning to the first one, this was registered as three separate pecks.

Experiment 5.4 - Consumption of food items of different shapes

This experiment was carried out on 34 chicks on four dates between 25th and 30th May 2008. Chicks were tested after completing one of the behavioural experiments described in Chapters 3 and 4, such that they were incubator-hatched and naïve to food, but not to pecking at stimuli associated with feeding (i.e. models of adult heads). Each chick was individually presented with four different types of food in succession, the order of which was randomized. Every item was held with stainless steel forceps at eye level, and chicks were allowed to swallow if they chose to do so. The foods used were one piece of:

a. Tinned macaroni in cheese sauce (28 mm long x 12 mm diameter).
b. Tinned spaghetti hoops in tomato sauce (2 mm thick, 10 mm diameter).
c. Tinned spaghetti loops in tomato sauce (2 mm thick, 13 mm long, 7 mm wide).
d. Tinned spaghetti in tomato sauce (3 mm thick).

The tinned spaghetti was cut into lengths from 1 cm to 6 cm. Chicks were initially presented with the 1 cm piece, followed by successively larger pieces, until the length reached was either too long for them to swallow, or they showed no inclination to eat more spaghetti.

Experiment 5.5 - Measurement of earthworm colour

The colour of six representatives of six different common species of earthworm was measured in March 2007. These species were *E. foetida, Lumbricus castaneus, L. festivus, Aporrectodea caliginosa, A. longa* and *A. rosea*. They were all dug up from fields and parks in and around Cardiff where Lesser Black-backed Gulls and Herring Gulls are often seen to foot paddle, especially when the ground is moist. The worms were first lightly anaesthetised by placing them in sparkling water for approximately 30 seconds. The colour of each was then measured at three different points (the head, the tail and the region of the clitellum) on the dorsal and ventral surfaces. This was done with an Ocean Optics CHEM2000-UV-VIS fibre optic spectrophotometer, with an Avantes DH-2000 deuterium (215-400 nm) halogen (360-1700 nm) light source and calibrated with a WS-1 Spectralon diffuse reflectance standard.

5.3.1 Statistical treatment

Results were analysed in Minitab 15 (Minitab Inc., 2007), Resampling Statistics 3.0.7 (Resampling Stats Inc., 1995) and R version 2.8.1 (R Core Development Team, 2008). The additional R packages "nlme" (Pinheiro *et al.*, 2008) and "lme4" (Bates *et al.*, 2008) were used for mixed-effects models, while *post-hoc* multiple pairwise comparisons were undertaken with the "multcomp" package (Hothorn *et al.*, 2008). Graphical figures were prepared in R version 2.8.1 (R Core Development Team, 2008) and GraphPad Prism 2.01 (GraphPad Software Inc., 1996). All statistical tests were two-tailed, with the significance level set at 0.05. Values are given as arithmetic mean ± SE.

Chicks' responses in experiment 5.1 with different odorants were analysed with the Friedman's test. Sign tests were used to evaluate differences in the number of chicks choosing particular food items in experiment 5.3a. The repeatability of chicks' choices in experiments 5.3a and 5,3b was estimated after the method described in Lessels and Boag (1987), using the mean squares of a one-way ANOVA.

Resampling was employed to determine whether individual chicks showed any preference for pecking at Worms, Discs or Strips of chicken in experiment 5.3c, following the method described in Simon (1995). Six items were removed at random from a choice of 18 items (six Discs, six Strips and six Worms, as in the trial itself) and the number of each type tallied. This was repeated 64 times (once for each chick in the experiment). The total numbers of each type were then summed. This whole process was repeated

10,000 times, so that the proportion of totals as large or small as any specified value could be determined.

A similar technique was employed to establish if chicks showed a preference for eating any of the food items they pecked. In this case, n items were chosen at random from the set of six actually pecked by each chick (where n = the number of items actually eaten by that chick). The items comprising the n choices were then tallied. This was repeated 51 times, with a different set of six each time, and different values of n, for each of the 51 chicks that actually consumed any food items. The entire procedure was then repeated 10,000 times and the total number of items of each type that would have been "consumed" on the basis of a truly random choice summed in each instance.

Other data were primarily modelled using methods analogous to those described in section 3.3.3, with model simplification proceeding through stepwise deletion and comparison of the likelihood ratio statistic at each stage. In experiment 5.2 (bill tip items), three models were fitted. The first of these was a linear mixed-effects model (LMM) with the total number of pecks per trial as the response variable, and chick age, laying order, egg volume, experimental date, stimulus type and order of stimulus presentation as explanatory variables. This was followed by a general linearized mixed model (GLMM) with a binomial error of the proportion of pecks to either a stimulus model's gonys spot (excluding the SS), or elsewhere. A further GLMM with a binomial error was then fitted for the "food" stimuli only, assessing the proportion of pecks to the food item, and those that were aimed elsewhere. All these mixed models had chick identity fitted as a random factor.

In experiment 5.3a, where chicks were offered a choice of two stimuli, a GLMM with a binary response variable and binomial error was fitted. The response variable was coded 0 for choice of the plain food item, and 1 for choice of the striped food item in each test. In this analysis, the test number (i.e. first or second peck) was fitted as a random effect along with chick identity, with the former nested within the latter. Explanatory variables were chick mass (as a proxy for age), date, the name of the test concerned (i.e. striped pasta v. plain pasta), and the order in which it took place relative to the other binary choice experiments and experiment 5.3b, along with two-way interactions.

A similar GLMM was fitted for experiment 5.4, with food eaten (1) and not eaten (0) was the response variable. Explanatory variables were chick age, experimental date, and the food type (spaghetti, hoops, loops or macaroni), while chick was fitted as a random effect. A separate general linear model (GLM) with a quasipoisson error was fitted to examine the probability that spaghetti of different lengths was consumed, with chick age and experimental date as explanatory variables.

Ordinal logistic regression was used to determine which of the four food items offered in experiment 5.3b was pecked at first. The items were coded from 1 to 4, in order of size, and this was fitted as the response variable. Explanatory variables were object size, the position of the chosen food item (to the left or the right of the chick), whether the chosen strip of meat was a member of the inner (middle) or outer (edge) pair of food items on the four-pronged fork, and the order in which the experiment took place relative to the trials in experiment 5.3a.

5.4 RESULTS

Experiment 5.1 - Testing the possible role of olfaction in chick feeding

Results from 2008 could not be analysed as an insufficient number of chicks responded by "sleeping" when placed under the infrared heat lamp. In 2007, there was only a minimal response (maximum score of 1) by any of the chicks to any of the stimuli presented. There was no significant difference between the effects of the odour treatments (Friedman's test statistic = 0.91, d.f. = 3, *p*

= 0.822), or the responses of the chicks to these scents (Friedman's test statistic = 9.69, d.f. = 22, p = 0.989).

Experiment 5.2 - Diverting chick pecking from the gonys spot

Linear models revealed that the type of head model presented had a significant effect on chicks' pecking response (LMM, $F_{5,125}$ = 16.95, p < 0.0001) (Fig. 5.5).

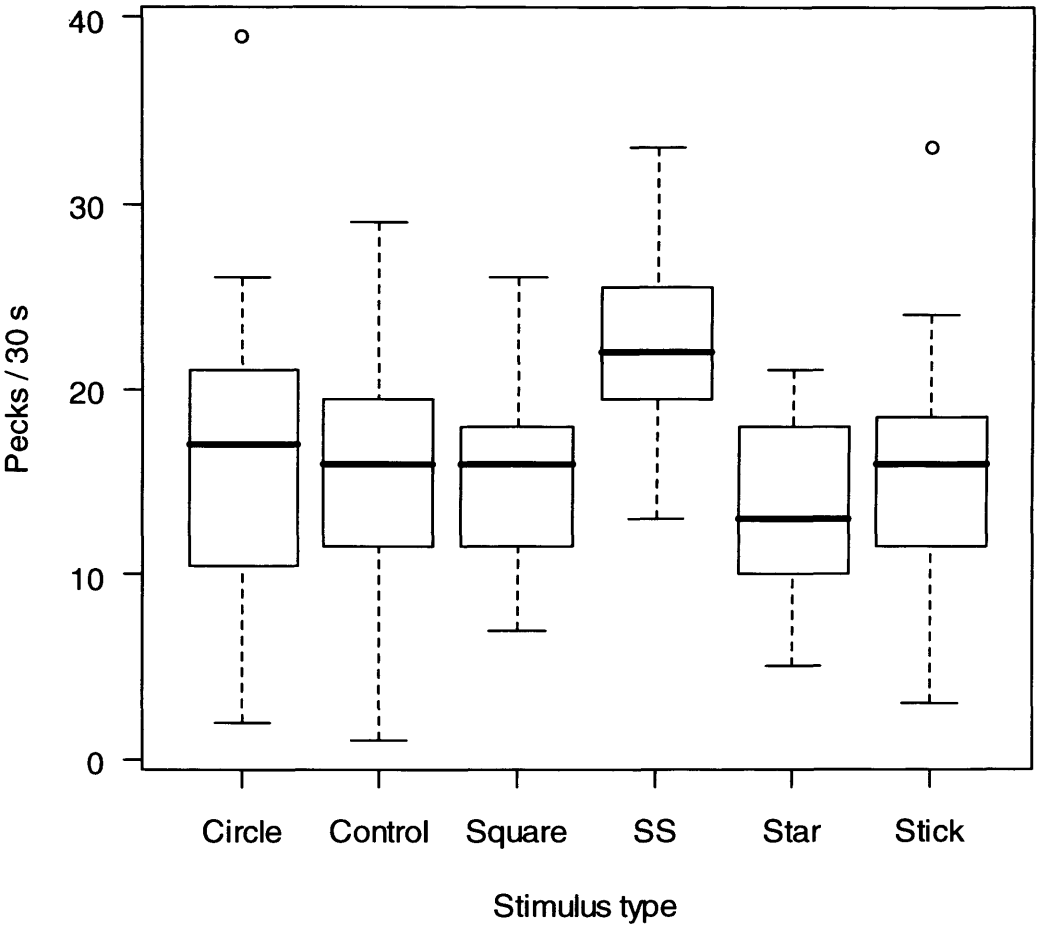


Fig. 5.5. Pecking responses in experiment 5.2, where different shapes were appended to the bill tips of model heads. Chicks pecked at a significantly higher rate to the SS than to any of the other stimuli, none of which elicited a significantly different response from each other.

Multiple pairwise comparison showed that this was due to the SS (22.44 ± 0.88 pecks) eliciting a significantly greater number of pecks than any of the other stimulus types (Circle – 16.37 ± 1.46, Control – 15.37 ± 1.29, Square – 15.19 ± 0.97, Star – 13.93 ± 0.93, Stick – 15.22 ± 1.20) (Table 5.1).

Comparison	Estimate*	z	*p*
Control – Circle	-1.00	-0.81	0.9660
Square – Circle	-1.19	-0.96	0.9320
SS – Circle	6.07	4.90	**<0.0001**
Star – Circle	-2.44	-1.97	0.3590
Stick – Circle	-1.15	-0.93	0.9400
Square – Control	-0.19	-0.15	1.0000
SS – Control	7.07	5.70	**<0.0001**
Star – Control	-1.44	-1.17	0.8540
Stick – Control	-0.15	-0.12	1.0000
SS – Square	7.26	5.85	**<0.0001**
Star – Square	-1.26	-1.02	0.9130
Stick – Square	0.04	0.03	1.0000
Star – SS	-8.52	-6.87	**<0.0001**
Stick – SS	-7.22	-5.82	**<0.0001**
Stick – Star	1.30	1.05	0.9030

Table 5.1. LMM pairwise comparisons of mean estimates. *p*-values adjusted for multiple comparisons. * S.E.=1.24. Significant values in bold.

There was also a significant effect of stimulus presentation order (LMM, $F_{5,125} = 11.23$, $p < 0.0001$), with more pecks directed at the first stimulus (20.48 ± 1.95) than at all stimuli presented subsequently (second – 16.96 ± 1.26, third – 15.81 ± 1.06, fourth – 13.93 ± 1.19, fifth – 16.96 ± 1.32, sixth – 14.37 ± 1.24) (Fig. 5.6).

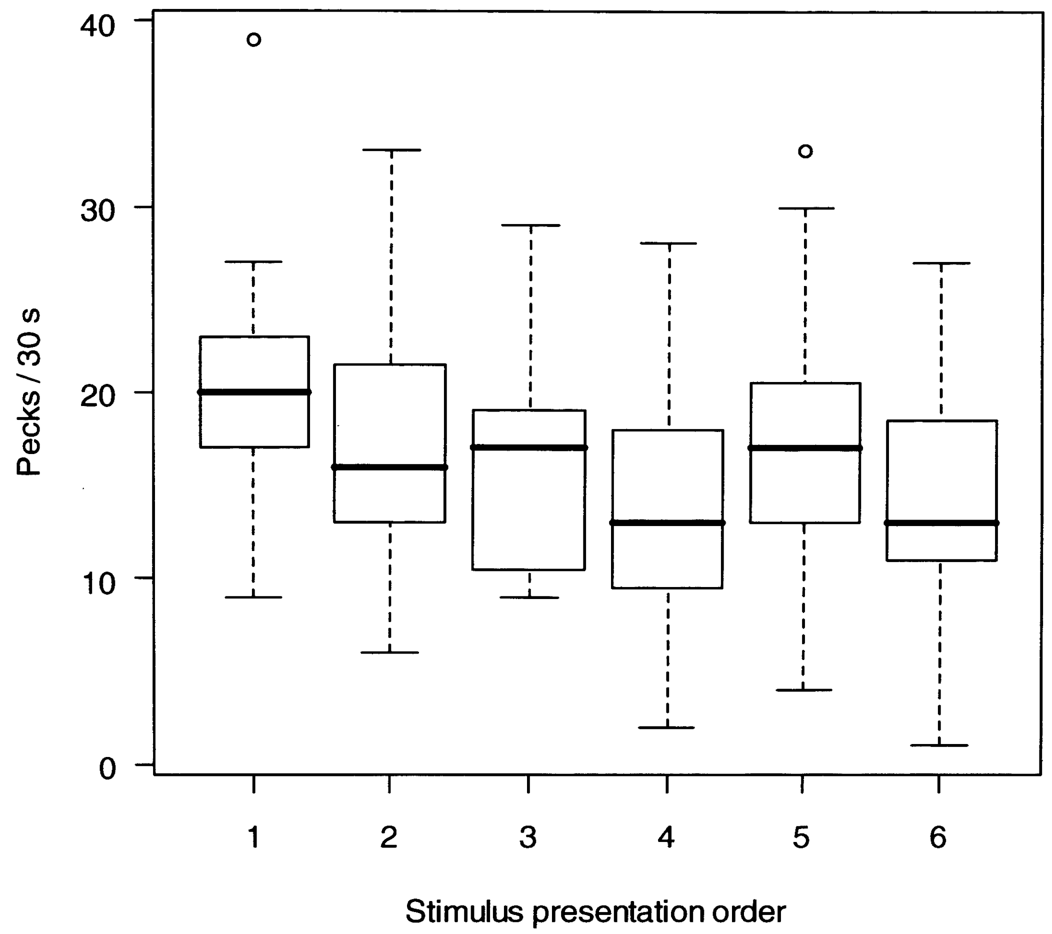


Fig. 5.6. The relationship between stimulus presentation order and chick pecking rate. There was a significant habituation effect in chicks' responses to successive stimuli in experiment 5.2.

Analysis of the position of pecks for all stimuli apart from the SS showed that the proportion of pecks aimed at the gonys spot compared to elsewhere varied significantly between stimuli. 21.0% of pecks were aimed at the spot for the Circle stimulus type, compared to 64.1% for the Control, 14.6% for the Square, 32.2% for the Star and 26.0% for the Stick. The Control models had a significantly higher proportion of pecks to their gonys spot than the Circle models (GLMM, z = 12.49, p < 0.0001), as did the Star models (GLMM, z = 3.54, p = 0.0004). Chicks directed a significantly smaller proportion of pecks to the gonys spot on the Square models than they did to the Circle models (GLMM, z = -2.44, p = 0.0146). The primary reason for the differences in the positioning to pecks between the food models and the Controls was that pecks to the former were directed to the food items at the end of the beak.

Of the pecks to the "food" models, 71.5% were aimed at the food for the Square models, compared to 62.3% for the Stick models, 57.7% for the Star models and 55.7% for the Circle models. These proportions were significantly different for the Square and Circle models (GLMM, $z = 4.92$, $p < 0.0001$) and the Stick and Circle models (GLMM, $z = 2.31$, $p = 0.0207$). There was no significant difference between the proportion of pecks directed at the food item for the Circle and Star models.

Experiment 5.3 - Assessing chicks' choices of plain or striped food items

5.3a Binary food choices

Sign tests showed that overall there was a significant trend for chicks to choose the striped stimulus for both the first (119 of 180 pecks to striped food, $p < 0.0001$) and second (121 of 180 pecks to striped food, $p < 0.0001$) pecks in each of the choice trials. Chicks' choices were highly repeatable between the first and second pecks in all trials (ANOVA, worm v. plain: $F_{61,62} = 28.93$, $p < 0.0001$, $R = 0.93$; plain pasta v. striped pasta: $F_{60,61} = 24.52$, $p < 0.0001$, $R = 0.77$; striped meat v. plain meat: $F_{61,62} = 28.09$, $p < 0.0001$, $R = 0.82$). A GLMM found no significant effect of any factors or covariates on the pattern of pecking observed, such that choice of striped food items was extremely robust.

5.3b Choice of four stimuli

In 46.8% of tests, a chick's first peck was at the largest food item, while the second largest piece of meat was chosen first in 25.8% of trials. The preference for the largest item rose to 76.0% in those trials in which the largest item was one of the two closest to the chick (i.e. a member of the middle pair of stimuli on the fork during stimulus presentation). The most highly significant explanatory variable was the position (inner or outer) of the chosen item ($z = -4.11$, $p < 0.0001$), such that chicks were significantly more likely to peck at items closest to their beaks (one of the middle pair of the fork), than those further away. The next strongest effect was the size of the item, with larger items emerging as more attractive than smaller items ($z = 3.36$, $p = 0.0010$). Experimental order also had a significant effect, with chicks less likely to peck at large food items if they took part in this experiment late in the sequence of trials ($z = 2.30$, $p = 0.0220$). There was no significant effect of side (left or right) on chicks' pecking choices. Chicks' choices were repeatable between the first and second pecks (ANOVA, $F_{61,62} = 146.99$, $p < 0.0001$, $R = 0.64$).

5.3c Pecking and eating choices of several different food items

Chicks showed a preference for pecking at the Discs (41.9% of pecks) over the Worms (34.1%) and the Strips (24.0%). The probability of a percentage as high as (or higher than), that seen for the Discs occurring through random choice alone was less than 0.0001. The probability of a percentage as high as (or higher than) that achieved by Worms was 0.3790, and as low as (or lower than) that achieved by Strips was 0.0001. Thus, there was a clear preference for pecking at the Discs, and a significant avoidance of Strips, while there was no significant trend for pecking at Worms.

The situation was rather different, however, when it came to the items actually eaten. Of those Worms pecked, 70.6% were eaten, compared to 38.6% of Discs and 36.8% of Strips. This meant that Worms were the most frequently eaten item overall (46.8%), followed by Discs (35.1%) and Strips (18.2%). The probability of a percentage as high as (or higher than) that achieved by Worms occurring by chance was less than 0.0001, likewise for a percentage as low as (or lower than) that achieved by Strips. The likelihood of as few, or fewer, Discs being consumed was 0.0615. Thus, Worms were definitely consumed more often than expected, and Strips less often, and there is also an indication that Discs were not consumed as often as the frequency with which they were pecked might suggest.

The difference between chicks' selections of what to peck and what to consume was illustrated by dividing them into two groups – "big eaters" and "small eaters" (Fig. 5.7). Small eaters tended to peck rather than eat, and pecked most frequently at the Discs (which were the same size as the parental bill spot). Big eaters, however, ate two thirds of the food items they pecked at, and pecked (and therefore predominantly ate) the Worms.

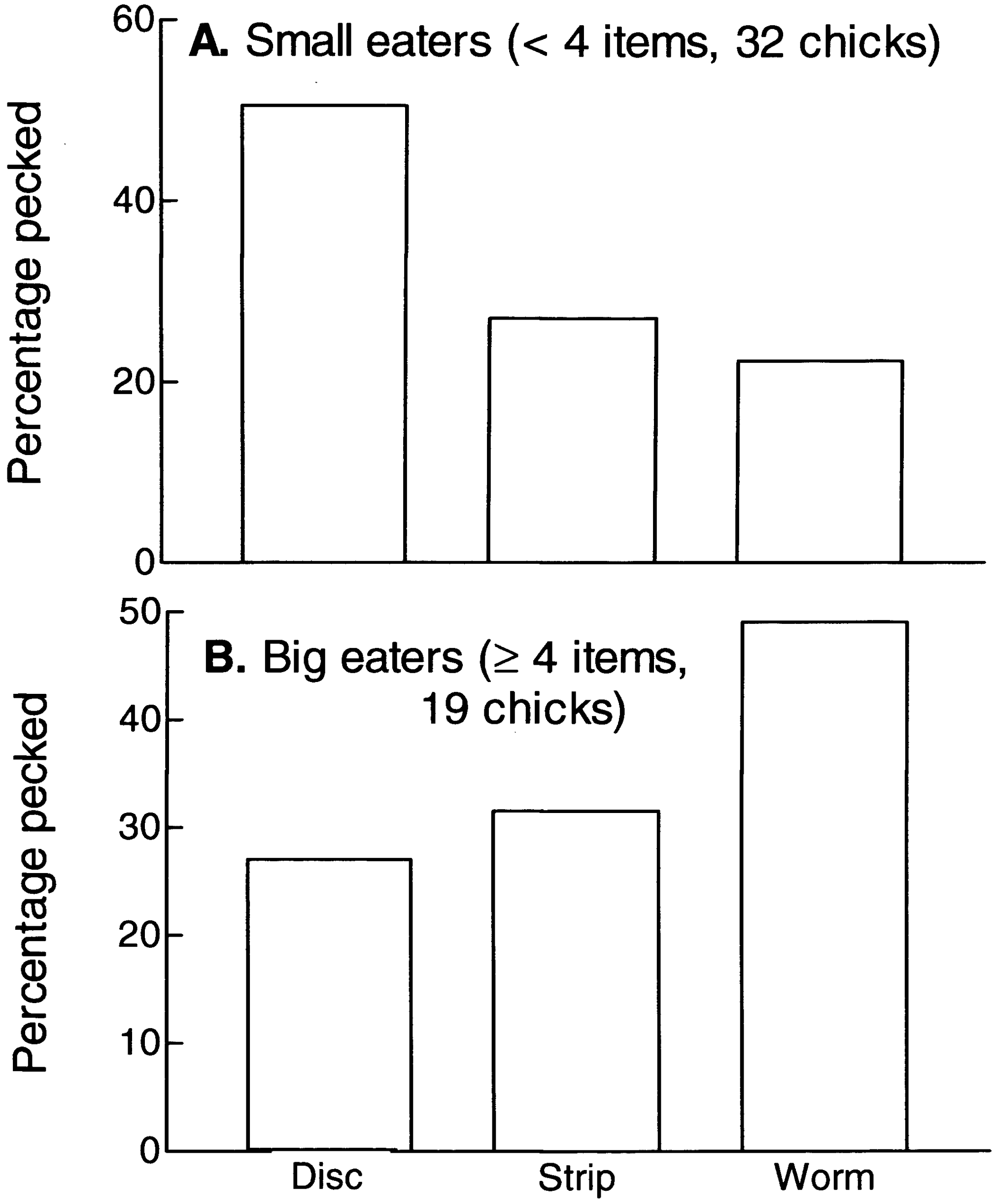


Fig. 5.7. Chicks' choice of items to peck in experiment 5.3c, divided into those that ate less and more than 50% of the items presented. The Discs were the most effective stimuli overall at eliciting pecks. However, those chicks that consumed the largest number of food items, and were thus presumably motivated by hunger, predominantly chose to peck the Worms.

Experiment 5.4 - Consumption of food items of different shapes

Sign tests showed that chicks were significantly more likely to eat hoops, loops and macaroni successfully than they were to fail ($p < 0.0001$ in each case), with only two of the 34 chicks (5.9%) tested not consuming hoops and macaroni, and three of 34 (8.8%) failing to swallow loops. However, this was not true for spaghetti, with only 16 out of 34 chicks (47.1%) eating at least a 1 cm length ($p = 0.8640$).

A GLMM revealed that of all the explanatory variables considered, only the type of food on offer influenced whether it was consumed, as spaghetti was swallowed significantly less often than the other food classes (GLMM, z = -3.72, $p = 0.0003$). Chick age almost had a significant effect (GLMM, z = 1.80, $p = 0.0722$), and the AIC was lower when age was retained in the model than when it was excluded (103.87 against 105.15). Further analysis of the spaghetti effect showed that there was a positive association between chick age and the length of spaghetti consumed (GLM, z = 3.16, $p = 0.0016$), although many chicks of all ages did not eat spaghetti at all (Fig. 5.8).

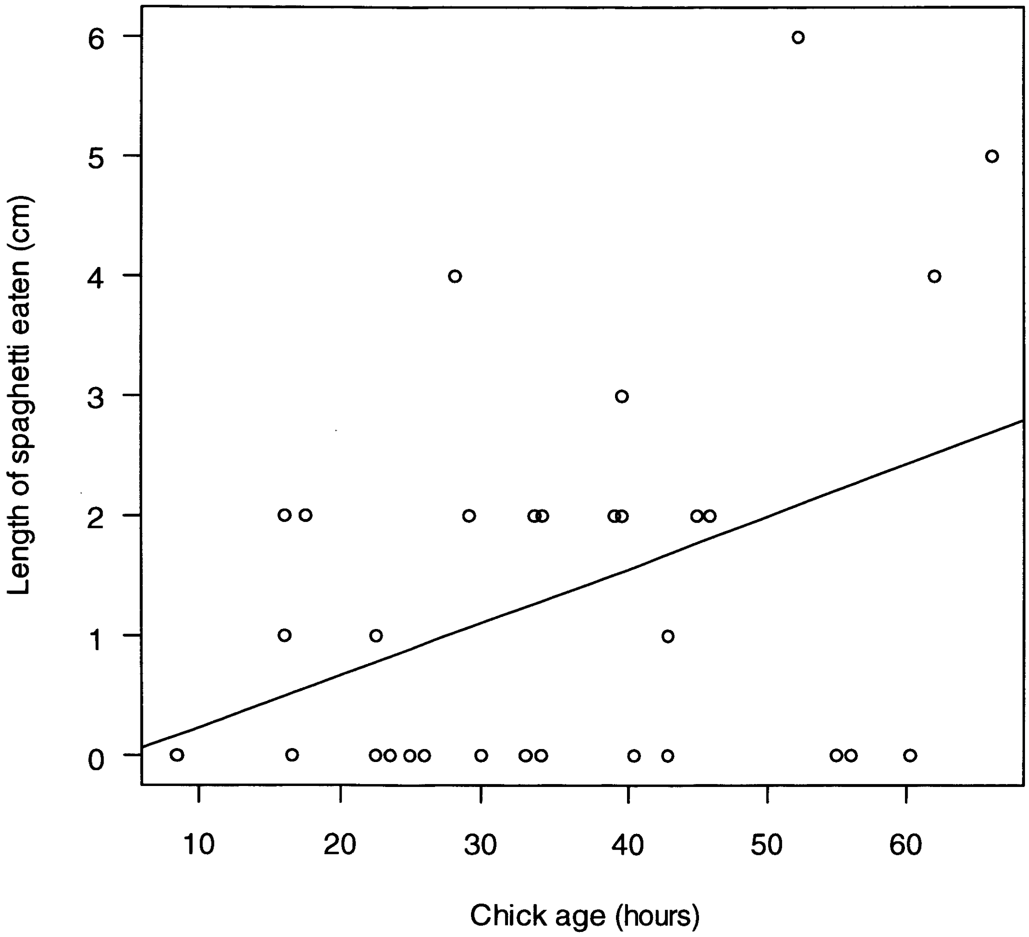
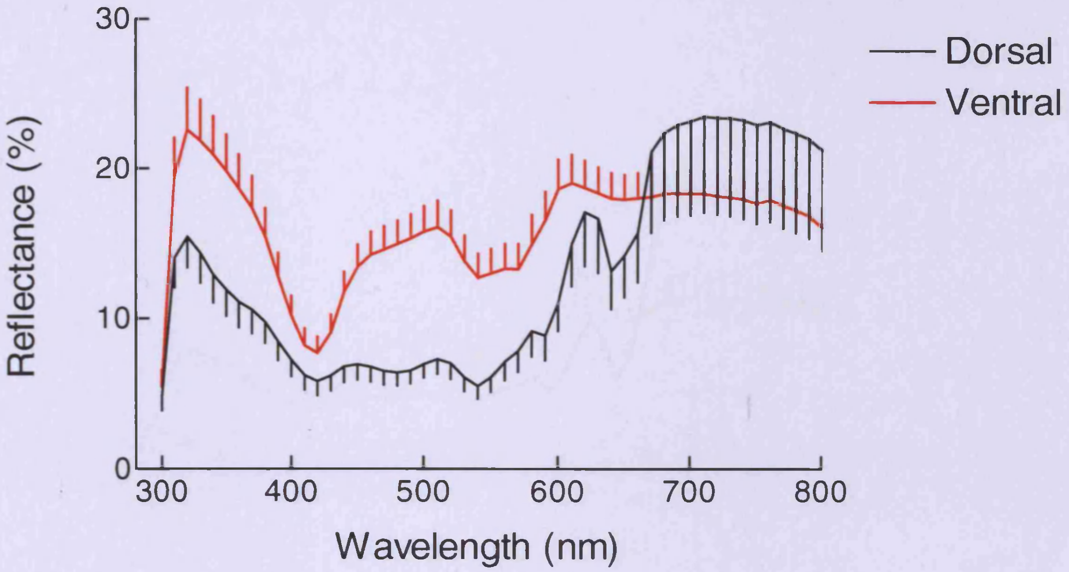


Fig. 5.8. The relationship between chick age and length of spaghetti eaten in experiment 5.4. The length of spaghetti consumed and probability of consumption was positively related to increasing chick age.

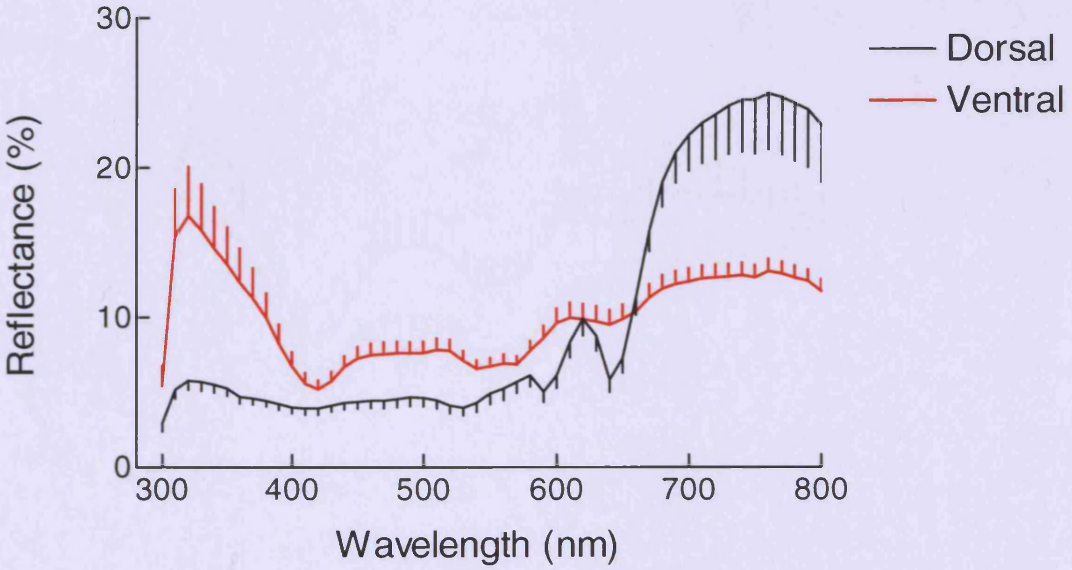
Experiment 5.5 - Measurement of earthworm colour

Worms of all species except *A. rosea* showed a distinct peak in reflectance at longer wavelengths on their dorsal surface (Fig. 5.9). They also all had a peak in the UV part of the spectrum, although in *E. foetida* (Fig. 5.9a) and *A. longa* (Fig. 5.9e), this peak was more pronounced on the ventral than the dorsal surface of the worm's body, and in *L. castaneus*, (Fig. 5.9b) and *L. festivus* (5.9c) the peak was only apparent on the ventral side.

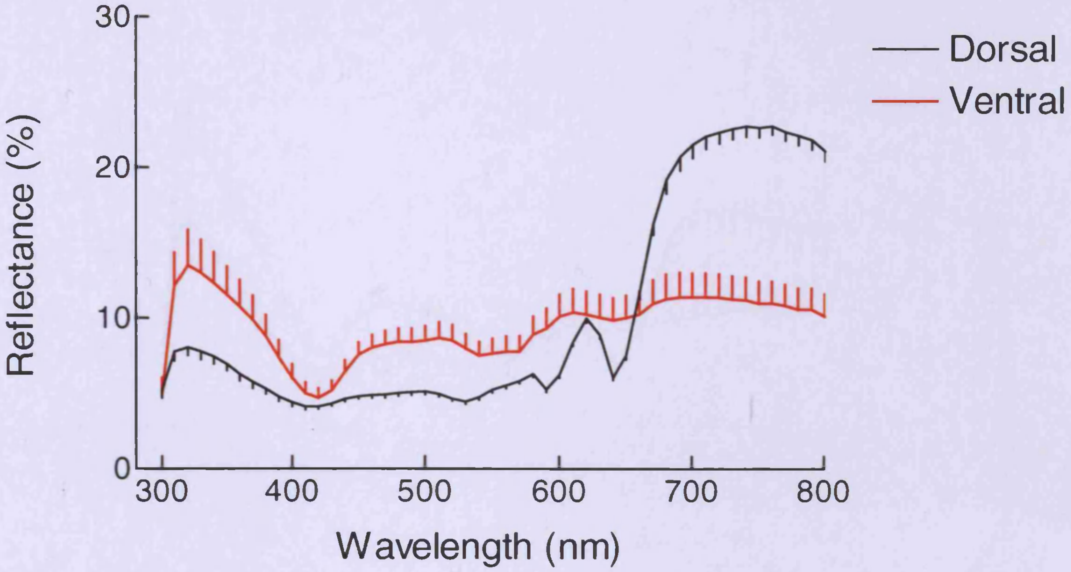
(a) *Eisenia foetida*



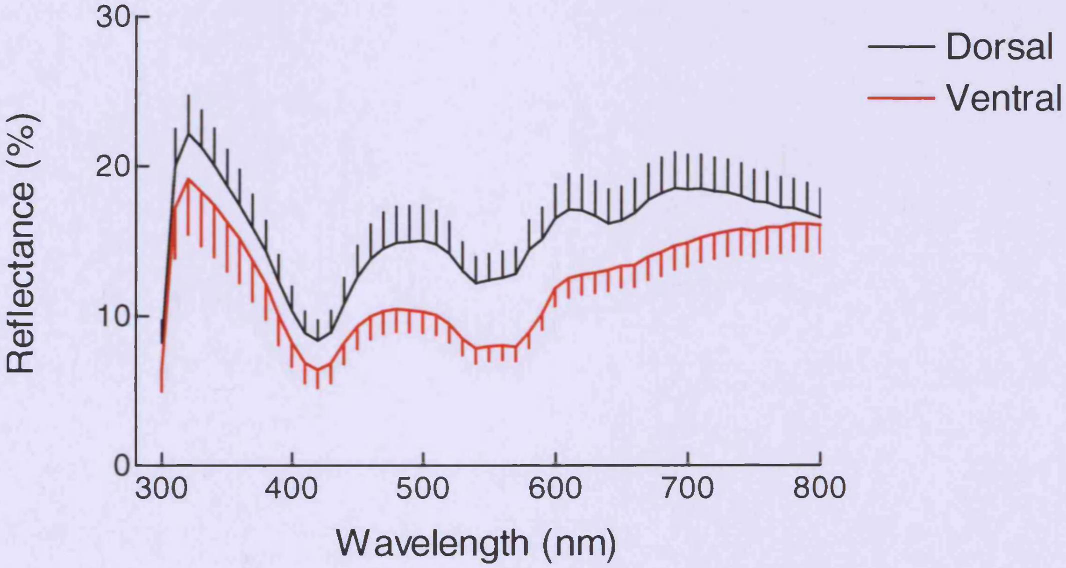
(b) *Lumbricus castaneus*



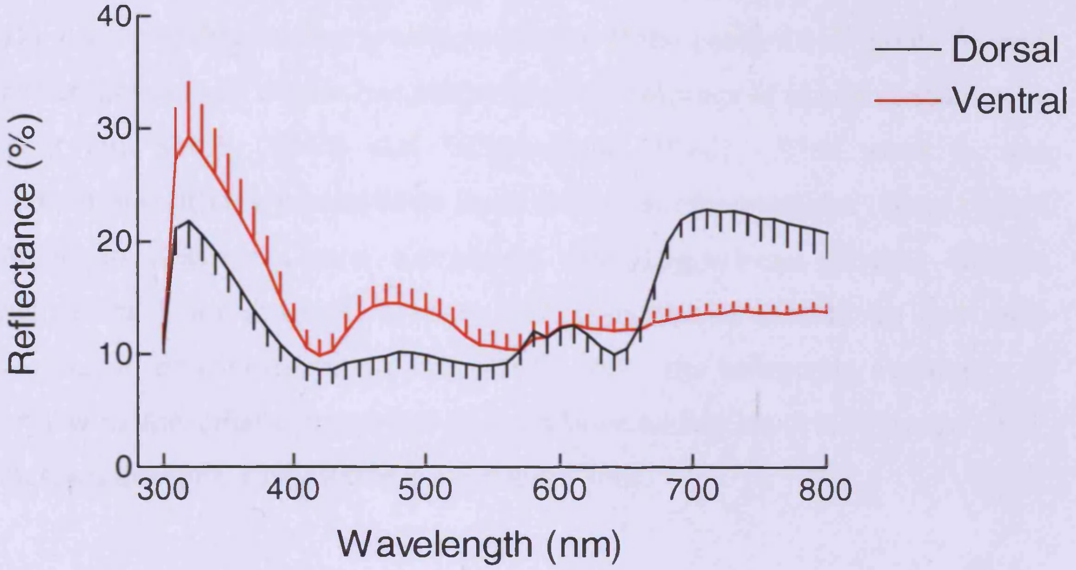
(c) *Lumbricus festivus*



(d) *Aporrectodea caliginosa*



(e) *Aporrectodea longa*



(f) *Aporrectodea rosea*

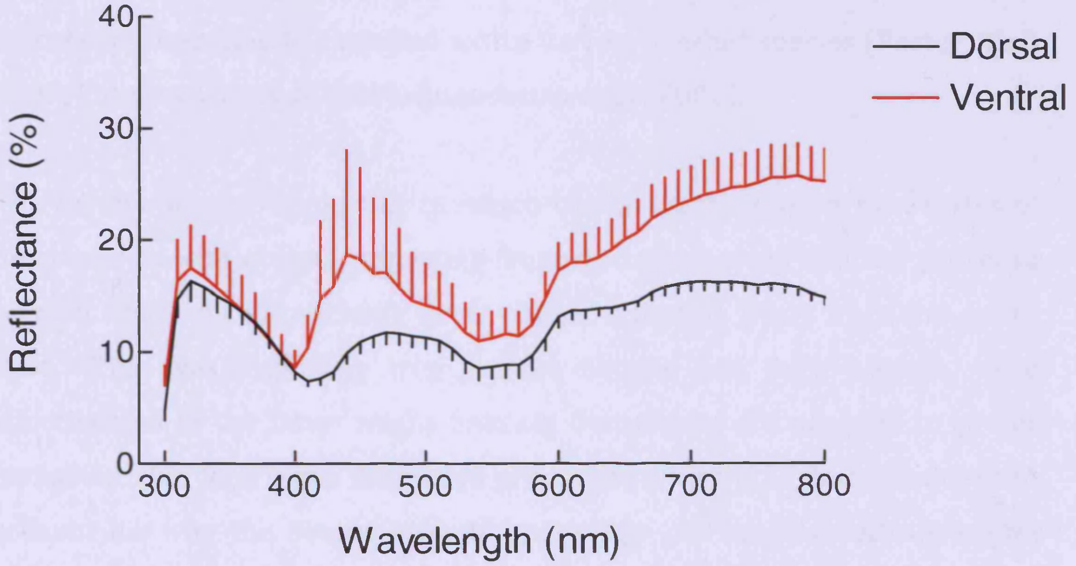


Fig. 5.9. Spectral reflectance of the dorsal and ventral surfaces of six species of British earthworm. Lines show mean ± S.E.

5.5 DISCUSSION

The results of this chapter provide evidence of the presence of innate feeding preferences in gull chicks, complementing the findings of previous studies by Hunt and Smith (1964) and Rabinowitch (1968). This work is also compatible with the results from studies of other avian species. Hand reared American Kestrels (*Falco sparverius*) and Loggerhead Shrikes (*Lanius ludivicianus*), for example, execute well coordinated attacks on live mice without prior experience (Smith, 1973), while the unlearned avoidance of prey with aposematic properties has also been widely reported (Smith, 1975; Marples & Roper, 1996; Rowe & Guilford, 1996).

Although gull chicks appeared to recognize food items (experiment 5.3c) no evidence was found that chicks use olfaction in this process (experiment 5.1), since there was no significant response to any of the odours presented. However, several chicks were not induced to sleep, indicating that this experiment was not a good test of their olfactory abilities, despite the fact that the method used has worked with a variety of other species (Porter *et al.*, 1999; Cunningham *et al.*, 2003; Bonadonna *et al.*, 2006).

The results of experiment 5.2, in which chicks were exposed to a series of head models with objects projecting from the bill, showed that the presence of such items did significantly draw chicks' attention away from the gonys spot. This was especially true for the Square and Stick objects. The effectiveness of the latter might indicate that chicks are adapted to prefer elongated, thin food items that share properties with the SS, but this does not account for why the Square was so appealing. All models with an object protruding from the bill elicited a level of pecking statistically equivalent to that of the Control, and were significantly less attractive than the SS despite the chicks having two targets to stimulate pecking. The echoes Hailman's (1967) result, in a test of the response of Laughing Gull (*L. atricilla*) chicks to several two-dimensional head stimuli, including one with "food" in the bill.[45] These findings indicate that the presence of items in the bill does not tap into the neural circuits controlling the supernormal pecking response (4.1.3). However, this result does not therefore provide direct evidence against the hypothesis that the supernormal response is an adaptation to chick feeding, as neither the food normally regurgitated for chicks, nor the SS, greatly resemble the shape or colour of the objects attached to the bill in the models used in this experiment. Also, although adults do sometimes hold food in the bill for their chicks (Tinbergen, 1953; Evans, 1970; Henderson, 1975), they often just regurgitate it on to the ground. This, combined with the unnatural appearance of the "food" stimuli, mean that it is not clear whether the chicks in the experiment were responding with feeding behaviour. A test involving more realistic stimuli, perhaps photographs of food items projecting from the model bill, might therefore be more appropriate. There was an effect of stimulus presentation order in this set of experiments, with the first presented stimulus receiving significantly more pecks than subsequent stimuli. This was also seen in similar experiments described in Chapter 4 and is discussed therein (section 4.4.2).

The experiments examining chick feeding behaviour (experiments 5.3 and 5.4) suggest that chicks are perfectly capable of feeding themselves, with little input resembling that given by the parents, from a very young age. It should be noted, however, that the naïve chicks used in experiment 5.4 might have been primed to behave appetitively by taking part in behavioural experiments beforehand, while those in experiment 5.3 could not be guaranteed naïve. Nevertheless, chicks typically responded vigorously to food with little encouragement despite the unnatural experimental setting.

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[45] Tinbergen and Perdeck (1950) reported a "considerable influence of food" upon comparison of Herring Gull chicks' responses to a bill model and a bill model with a disc of "food" attached to the top. However, they did not use statistical tests to assess the difference in chicks' reactions to the stimuli used.

The results of experiment 5.3b suggest that chicks prefer larger food items, which, although adaptive to maximizing their energetic needs, is not necessarily consistent with the hypothesis that chicks are adapted to prefer small foods as delivered by their parents in early life. However, chicks' choices in these trials were primarily mediated by how close the stimuli were.

It is perhaps interesting that the chicks in experiment 5.4 consumed pasta hoops, loops and macaroni more enthusiastically than they did lengths of spaghetti that were smaller in size than any of the former. This implies that young chick feeding behaviour is not always constrained by food size, (indicating that the results of experiment 5.3b might be adaptive), and there were hence other properties of the spaghetti that rendered it less likely to be eaten than the larger pasta shapes. In most cases the spaghetti was not taken because the chicks concerned showed no interest in eating it, rather than because they tried and failed to swallow it, suggesting that it was inherently less attractive to the chicks than the other foods offered.

Further evidence of this effect is seen in the results of experiment 5.3. Here it appeared that gull chicks innately preferred to peck at striped food items when provided with a choice between these and plain food. This was seen in all binary choice trials (experiment 5.3a), and was consistent both between the first and second pecks in a given trial, and between the different choices available. The fact that no candidate variables significantly affected the nature of the choices made, suggests that these preferences are extremely hard-wired in young chicks, and as such were not affected in the way that other experiments detailed in this thesis were by factors like age or stimulus presentation order. The preference for stripes was even seen when their appearance was mediated by texture only rather than by colour, in the case of the pasta, indicating a well-developed sensitivity for this type of pattern in small chicks. Stripes (or scales/segments) are properties of the food items switched to by parents feeding young chicks (i.e. small fish and invertebrates), providing some support for the hypothesis that chicks have innate feeding preferences related to these dietary switches. The preference for stripes is particularly striking considering that the chicks used in these tests could not be assumed to be naïve, and might have thus begun to develop a preference for foods of a difference appearance if such items had delivered by their parents, in a process of vertical transmission of foraging practices (Annett & Pierotti, 1999) (although these chicks appeared to be very young, so extensive feeding was unlikely).

In experiment 5.3c, where chicks were able to both peck and consume a choice of three different food types, a slightly different trend emerged. The Discs received the highest proportion of pecks, but the Worms were eaten preferentially. In both cases, the Strips were avoided at a level greater than that predicted by chance. The circular shape of the Discs might have been effective at eliciting pecks because of its shared dimensions with the parental gonys spot towards which chicks of the age tested are predisposed to peck (Tinbergen & Perdeck, 1950). Chicks that ate a large number of items preferentially pecked (and ate) Worms, however, indicating both recognition and choice of striped food when motivated by hunger. Of course, as the chicks involved could not be considered naïve, it is possible that they might have already eaten worms and developed a learned preference for them, but all appeared to be newly hatched, so this is improbable. Taken together with experiment 5.3a, these results echo Rabinowitch's (1968) findings of an innate preference for worms (which would be especially true if the chicks tested had begun to be fed different foodstuffs by their parents, in a process analogous with the training Rabinowitch's (1968) birds were subject to in his experiments).

Colour measurements of earthworms showed that all species have distinct peaks in the UV on their ventral surfaces, and in all but the *Lumbricus* species, these peaks are seen on the dorsal surface too. Birds from a range of species are known to use UV cues in foraging (e.g. Honkavaara *et al.*, 2002), and there is speculation that gulls' UV-sensitive photoreceptors, which are thought to be a derived rather than an ancestral character state (Ödeen & Håstad, 2003), are an adaptation to terrestrial foraging (Håstad *et al.*, 2005). Since earthworms are amongst the terrestrial prey commonly taken by gulls of many species, and these results show they are reflective in the UV, gulls might therefore employ their UV-sensitive vision when hunting for earthworms. Indeed, the UV peaks of the worms would make them conspicuous on the sort of backgrounds against which they would be seen, such as leaf letter or green leaves, which predominantly reflect light at longer wavelengths (Andersson *et al.*, 1998). Birds have been shown to use such chromatic contrast in the UV reflectance of prey items and their backgrounds to aid foraging (Stobbe *et al.*, 2009). The UV reflectance of earthworms might therefore have provided a cue of comestibility to chicks, and might hence help explain the preference for earthworms over other food items observed in experiment 5.3c.

The results of experiment 5.3 provide some evidence that the supernormal pecking response occurs because the SS taps into chicks' innate feeding preferences, as the stripes so strongly preferred by the chicks (experiment 5.3a) are the most important element of this stimulus in bringing about this behaviour (experiments 4.2c and 4.2d). Moreover, the reddish colour of the worms eaten in experiment 5.3c, along their elongated shape, recalls the SS. These innate preferences could have arisen if chicks' dietary requirements in early life were met by striped or segmented food, or because any adaptation that facilitates feeding of the items commonly delivered by the parents would accrue a selective advantage over siblings in competition for food. If feeding preferences are connected to chicks' nutritional needs, this could relate to the dietary switch observed in several gull species at this time, with chicks' either adapting to the food typically brought by their parents, or parents attending to their chicks' innate preferences. The latter could be promoted by the rejection of unsuitable food items by chicks (Pierotti & Annett, 1987; Annett & Pierotti, 1989), or the form of begging characteristic to young chicks (Ferns & Ross-Smith, 2009), although this would appear to be an inefficient (and thus selectively disadvantageous) way of rearing chicks. It is perhaps significant that dietary switches have largely been recorded in the monophyletic clade within the large white-headed gulls, in which species have a red spot at the gonys (Table 5.2). In these species, chicks are small relative to their parents at hatching (Ferns & Ross-Smith, 2009), hence the delivery of appropriate foods to chicks could be even more imperative for this group than for the other gulls, as fast growth might facilitate avoidance of predation by the relatively large adults in the colony.

Species	Location	Young chick diet	Old chick/adult diet	Author(s)	Technique
L. argentatus	Memmertsand, Germany	Crabs	Bivalves	Goethe, 1937[¥]	
L. argentatus	Terschelling, Netherlands	Fish, crabs, worms	Bivalves	Tinbergen, 1953	O
L. argentatus	Frisian Is., Netherlands	Fish, crabs	Marine invertebrates	Spaans, 1971	O, P, R, S
L. argentatus	Storsundsharun, Finland	Fish	Refuse	Hillström *et al.*, 1994[*]	R
L. argentatus	Ailsa Craig, UK	Fish, worms	Meat	Nogales *et al.*, 1995	P, R
L. argentatus	Terschelling, Netherlands	Crabs, gull chicks	Fish, marine invertebrates (bivalves)	Bukacińska *et al.*, 1996[$]	P
L. smithsonianus	Lake Erie, USA	Fish	Refuse	Belant *et al.*, 1993	P, R
L. smithsonianus	Great Island, Canada	Fish	Refuse, mussels, seabirds	Pierotti & Annett, 1987	O, P, R
L. dominicanus	South Shetland Is., Antarctica	Fish, krill	Carrion	Favero & Silva, 1998	P, R
L. dominicanus	Patagonia, Argentina	Fish	Intertidal invertebrates (molluscs)	Bertellotti & Yorio, 1999	P
L. dominicanus	Gerlache Strait, Antarctic	Krill	Limpets	Silva *et al.*, 2001	P, R
L. dominicanus	Coquimbo, Chile	Fish	Refuse	Ludynia *et al.*, 2005[*]	P
L. michahellis	Mediterranean, France	More terrestrial food	Refuse	Duhem *et al.*, 2005	R
L. michahellis	Mediterranean, Spain	Small terrestrial/aquatic prey	Larger prey	Ramos *et al.*, 2009	R
L. fuscus	Flat Holm, UK	Worms	Refuse	Stanworth, 1998	O , R
L. occidentalis	Alcatraz Island, USA	Small fish	Refuse	Annett & Pierotti, 1989	O, P, R, S
L. hyperboreus	Eastern Alaska, USA	Terrestrial prey	Marine prey	Schmutz & Hobson, 1998	I, R, S
L. glaucescens	Aleutian Islands, USA	Fish	Intertidal invertebrates	Irons *et al.*, 1986	O, P, R
L. cachinnans	Tarnów, Poland	Fish	Refuse	Skórka, & Wójcik, 2008[*]	O
L. atlanticus	Golfo San Jorge, Argentina	Crabs	Crabs	Herrera *et al.*, 2005	P
L. delawarensis	Gull Island, Canada	Insects, worms	Fish	Kirkham & Morris, 1979	O, R
L. canus	North Sea, Germany	Crabs, worms, fish, insects	Crabs, worms, fish, mammals, fruit	Kubetzki *et al.*, 1999[*¤]	F, P
I. audouinii	Chafarinas Is., Spain	Terrestrial invertebrates	Fish	Pedrocchi *et al.*, 1996	R
C. novaehollandiae	Wollongong, Australia	Natural foods	Refuse	Smith & Carlile, 1993[§]	R

Table 5.2. Dietary switches in gulls. [¥] Cited in Tinbergen (1953). [*] Switch inferred from adult diet only. [$] Switch found in successful pairs only. [¤] Switch varied with colony location. [§] Few regurgitates taken from chicks, so switch primarily inferred from adults.
F – faeces analysis, I – stable isotope analysis, O – observations, P – pellet analysis, R – regurgitations, S – stomach content analysis.

Chapter 6

General discussion

6.1 MAIN FINDINGS

This thesis set out to investigate the pecking response of gull chicks, and to elucidate the role of genetic, parental and environmental factors in shaping this behaviour. Particular attention was given to the supernormal pecking response, to try and understand whether it is a consequence of adaptive or non-adaptive processes.

The work described in Chapter 2 laid the foundations for this work. The careful monitoring of the colony allowed quantification of a number of possible predetermined variables that might have influenced chicks' pecking behaviour, such as egg volume and laying date. The method developed for hatching and temporarily rearing naïve chicks in a controlled environment further meant that the effect of post-hatching experience on the pecking response could be assessed, along with changes that emerged spontaneously with age.

The main findings of Chapter 3 indicated that on the whole newly hatched chicks pecked at simple models of adult heads, regardless of the appearance of key features, such as the colour, size, position, and even the presence of the gonys spot. Chicks were, however, sensitive to differences between the stimuli presented during the course of an experiment, responding less well to models with small and ill-defined gonys spots than to larger ones, or models with an extra circle added around their spot.

Chapter 4 demonstrated that a supernormal response of significant magnitude was found in Lesser Black-backed Gull (*Larus fuscus*) chicks. Maximum pecking was seen in response to superstimuli (SS) with a both a diameter and stripe width of approximately 3 mm, but there did not appear to be a marked difference between the releasing power of a SS with three stripes, compared to one with a greater number of stripes. Experiments in which the four elements of the SS were separated (the red colour, the length, the thinness and the three stripes) on different head models indicated that the white stripes were the key element in provoking supernormal pecking behaviour, followed by the red colour.

The results of Chapter 5 found no evidence that olfaction was involved in drawing chicks' attention to food. Objects between the bill tips of model heads, did, however, significantly redirect chicks' pecks away from the gonys spot, although their presence did not significantly affect the rate of pecking observed relative to the Control. Experiments with naïve chicks suggested that these birds have innate feeding preferences based on the shape of food items. Given the choice of foods, chicks also exhibited a strong and highly repeatable preference for items with stripes. Food size was also found to be influential in choice experiments, with chicks consistently selecting larger food items. There was also some indication that hungry chicks peck and eat worms preferentially, while more sated chicks simply peck items sharing properties with the gonys spot. Measurements of earthworms showed that several species had a distinct peak in the ultraviolet (UV), which might partly explain the attractiveness of worms, since the UV sensitive photoreceptors possessed by gulls are thought to be an adaptation to terrestrial foraging (Håstad *et al.*, 2005), during which prey items such as earthworms are regularly sought (Coulson & Coulson, 2008b).

6.2 INFLUENCES ON THE PECKING RESPONSE

6.2.1 External factors

One of the clearest trends to emerge from the results of all chapters was that the pecking behaviour assessed was very robust relationship to the predetermined variation measured between the chicks in terms of egg and parental quality. Apart from a very weak effect of laying order and egg volume seen in the supernormal pecking response of experiment 4.3a, no other external effects on chick responses were found. Thus, parental nest quality, distance of parental nests to neighbours in the colony, laying date, egg volume and laying order were all largely unimportant influencing the pecking behaviour of naïve newly hatched chicks from clutches of three eggs. This is likely to be adaptive, as the pecking response is absolutely fundamental to chick survival. Young chicks must peck effectively when their parents arrive to feed them, because if they fail to do so, they will die of starvation. The fact that pecking responses are found in a variety of precocial and semi-precocial species further indicates either that this behaviour is evolutionarily ancient, or that there has been strong selection for it to emerge several times through convergent evolution. In any case, it is likely that the pecking response of Lesser Black-backed Gulls as measured in this study has been fine-tuned by evolution, helping explain its relative imperviousness to external influences. Furthermore, the effects of factors such as chick survivorship as a function of laying order, are affected by the presence of siblings and hence the position in the brood hierarchy, as well as the skills of a chick's parents, none of which were explored through the experimental set-ups employed herein.

6.2.2 Ontogenetic influences

In contrast to the absence of extrinsic influences on the pecking response, there was an effect of chick age in experiments 3.5, 4.1 and 4.3b, (with naïve chicks), indicating spontaneous changes in chick pecking behaviour through the early stages of growth and development. The direction of this effect was towards a significant increase in pecking with age, which ranged between 3.8 and 48.3 hours post-hatching. This trend conforms to similar observations in Black-headed gulls (*Chroicocephalus ridibundus*) (Weidmann & Weidmann, 1958) and Ring-billed Gulls (*L. delawarensis*) (Iacovides & Evans, 1998). However, compared to the latter study, the findings of this thesis demonstrate an effect in younger chicks. The increase in response with chick age is likely to be a result of improved motor coordination of older chicks (Hailman, 1967) together with increasing levels of hunger, though chicks taking part in the experiments were still young enough to have had ample yolk reserves (Hailman, 1967; Hario *et al.*, 2004), and chicks in the wild are often not fed by their parents until they are several hours old (Tinbergen & Perdeck 1950, personal observation). Developmental changes in gull chick begging behaviour have been observed in other studies, although with a couple of exceptions (Collias & Collias, 1957; Hailman, 1967), most work has concentrated on chick development over a larger age range than that considered in this thesis, and hence the chicks involved were not naïve to food and bill stimuli (e.g. Moynihan, 1959; Margolis *et al.*, 1987; Alessandro *et al.*, 1989; Groothuis, 1989a; 1989b; 1992).

6.2.3 Effect of learning

In experiments with non-naïve chicks carried out in 2006 and 2009, mass was used as a proxy for chick age, and a decline in pecking rate with increasing mass was found in experiment 3.2. At first glance, this outcome might appear to contradict the findings discussed in the previous paragraph. However, the observed decrease in pecking is arguably due to experience rather than age. All the chicks in this experiment would have seen their parents, and some, particularly the heavier individuals, would have almost certainly been fed. These chicks might have thus begun to learn features of their parents' appearance and other cues associated with their presence (e.g. vocalizations, the nest site) (Beer, 1969b; 1970a; 1970b; Evans, 1970; 1986; Conover & Miller, 1981; Knudsen & Evans, 1986; Griswold *et al.*, 1995; Charrier *et al.*, 2001; Mathevon *et al.*, 2003), and therefore recognized both the models used and the experimental environment as alien. This effect is underlined in the results of experiment 3.1, where chicks' responses to two-dimensional models decreased with increasing mass, but the opposite relationship was seen towards three-dimensional models and real adult heads, with the trend more pronounced in the latter than in the former. These results again suggest that the heavier chicks were responding more enthusiastically to models that bore a greater resemblance to their parents, while younger, lighter chicks, responded more to the two-dimensional models, possibly because they possessed clear, simple features, than to the more complex attributes of the three-dimensional models and real heads.

The speed at which chicks can modify their responses upon exposure to stimuli was clearly seen in the results of many of the experiments in Chapters 3, 4 and 5. There was a consistent effect of learning in these experiments, which brought about rapid adjustments of chick behaviour in response to successive stimuli.

Stimulus presentation order significantly affected chick responses in experiments 3.4, 4.1, 4.2d and 5.2, such that if a stimulus was one of the last encountered during the experimental procedure, it was pecked significantly fewer times than if it was one of the first. This habituation effect backs up Tinbergen and Perdeck's (1950) own observation of "negative conditioning" upon repeated exposure to stimuli. However, unlike this study, and subsequent reports of similar phenomena (Nyström, 1973; ten Cate *et al.*, 2009), the findings reported in this thesis show a decline in responsiveness to stimuli over the course of experiments in which chicks were presented with each stimulus type on a single occasion, and when they were given relatively lengthy breaks between trials. This suggests that chicks were perhaps habituating to the environment in which experiments were carried out, or learning through conditioned inhibition that the experimental set-up predicted the absence of food. Such rapidly formed associations with the experimental environment would be compatible with reports from the wild that chicks quickly learn the features of their parental nests (Noseworthy & Lien, 1976; Conover & Miller, 1981). It is also possible that chicks habituated or became conditioned to cues shared by several of the stimuli presented, such as the eye, although this seems unlikely as no decline in pecking was seen in experiment 4.2c, where models had many features in common, while conversely, a decrease was seen in experiments where models were much more dissimilar to each other, for example experiments 4.1 and 4.2d.

Further evidence of how chicks' sensitivity to stimulus exposure affects their responses to different stimuli can be seen in the results of experiment 3.5, where chicks' responses to the Control were altered by the nature of the other stimuli presented in the experiments. In experiment 4.2c, in which one element of the SS was added to a series of head stimuli, there was a lower response to the Control in than in experiments 4.1, 4.2d and 5.2. In contrast, the level of pecking to the Control in experiment 4.2d, involving the removal of one element of the SS from a series of head stimuli, such that each had three features of the SS, was higher overall than for experiments 4.1, 4.2c and 5.2. The difference between the pecking seen in experiment 4.2c and experiment 4.2d was significant, with approximately twice the number of pecks seen to Controls in the latter than in the former.

These results suggest that the presence of so many SS features on five of the six stimuli used in experiment 4.2d heightened the chicks' motivational state, therefore increasing their pecking rates towards the Control, even though this stimulus lacked all of the distinguishing features of the SS. The depression in response to the Control seen in experiment 4.2c is harder to explain. It might indicate that with only one element of the SS present on most of the other stimuli (four out of six), the chicks' motivational state was not elevated to the same extent. Rather, exposure to components of the SS might have primed chicks to perceive the contrast between the Control and more attractive stimuli, that is the SS, Red and Stripes models (the only ones that increased pecking rate), such that they reduced the pecks they gave to the Control accordingly. Experiments with juvenile Herring Gulls have demonstrated that these birds show a high degree of discrimination learning, responding rapidly to differences between stimuli (Benjamini, 1984), so it is possible that similar mechanisms were operating in experiment 4.2c. It is unlikely the depression observed was the result of habituation to non-supernormally stimulating Control features, as it was not seen in experiment 5.2, where all heads used were identical to the Control, except for the addition of objects to the bill tips.

Taken together, these results suggest that although some stimuli are preferred to others, there is a relative lack of specificity in the stimuli releasing pecking behaviour in very young, naïve chicks. Chicks in this study pecked enthusiastically towards a range of stimuli of different shapes, sizes and colours, many of which were neither similar to the adult bill, nor the SS. The insensitivity of young chicks to the features of head stimuli is perhaps most starkly illustrated by the results of experiment 3.4, where chicks pecked equally well at a range of head models, even though some of these completely lacked key features, such as the gonys spot or the gape, or had the position of these features altered. This result is reminiscent of findings from studies with Laughing Gulls (*Leucophaeus atricilla*) and American Herring Gulls (*L. smithsonianus*), showing that chicks pecked at models in which the features of the entire head were mixed up (Margolis *et al.*, 1987; Alessandro *et al.*, 1989), suggesting that this lack of stimulus specificity might apply to a number of gull species. The initial flexibility in the objects releasing chick pecking might be adaptive to chicks in responding to natural variation in the appearance of breeding adults, such that chicks will peck their parents' bills even if they deviate slightly from that typically found (e.g. the gonys spot is small or diffuse). The rapid modification in pecking behaviour through experience, however, could be an adaptation for swiftly learning the features of parents, suitable foodstuffs (which could be advantageous in seizing food before siblings), and the appearance of the natal territory. Parental and territorial recognition might be especially important in ground-nesting colonial species such as the Lesser Black-backed Gull, in which chicks that wander outside the natal territory may risk death as a result of aggression from neighbouring adults (e.g. Paynter, 1949; Davis & Dunn, 1976; Brouwer *et al.*, 1995).[46]

6.3 PECULIARITIES OF THE SUPERNORMAL PECKING RESPONSE

Although many of the results discussed in the previous section apply equally to the supernormal pecking response and to behaviour directed towards more typical head-like stimuli, there were differences that set the behaviour released by the SS apart from the other responses recorded. The first of these was that supernormal pecking behaviour appeared to be more resistant to the effects of learning than was pecking towards non-supernormal stimuli. In experiment 4.3b, where the response to the SS was compared across several experiments, there was no effect of the other stimuli presented in the trials, and hence the response to the SS was consistently high. There was also no effect of chick mass on the supernormal pecking in experiments with non-naïve chicks (experiment 4.2a), in contrast to the observed decrease in pecking to Control heads observed

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[46] In species where intraspecific attacks on chicks are uncommon, such as the Black-legged Kittiwake (*Rissa tridactyla*), parental recognition (through auditory signals) by chicks is weaker than in ground nesting larids, suggesting that selection for learning parental features is relaxed (Mulard *et al.*, 2008).

in experiments 3.1 and 3.2. This suggests that the SS is so attractive that it transcends any neophobia that might set in as chicks age (Conover & Miller, 1981). It also indicates that chicks do not perceive the SS as a substitute for an adult head, because if this were the case, their responses might have been expected to decline with the onset of parental recognition. The positive relationship between pecking rate and advancing chick age also appeared stronger for the SS than for the head stimuli used, with a steeper gradient (experiment 4.1).

6.3.1 Tinbergen and Perdeck's hypothesis

Such distinctions between supernormal and "normal" pecking behaviour, indicate that chicks' responses to the SS and to head-like stimuli are controlled by separate mechanisms. If true, this would not support Tinbergen and Perdeck's (1950) hypothesis for explaining the evolution of supernormal pecking behaviour. Tinbergen and Perdeck (1950) suggested that supernormal behaviour was an adaptation to the ventral view by which young chicks initially see the bill of their parent directly prior to their first feed, when they are crouched in the nest shortly after hatching. The implication of this hypothesis is that responses to both the SS and to head stimuli relate to the parental bill, and are hence processed by the same neural mechanisms, such that the behaviour released by these stimuli should be of the same nature, albeit of a different magnitude.

There was also no support for Tinbergen and Perdeck's (1950) hypothesis in experiment 4.1 which was specifically designed to address this issue. The experiment carried out found no difference in chicks' responses to the Control and Ventral models, and both were significantly less attractive to chicks than was the SS. A result in agreement with Tinbergen and Perdeck's (1950) hypothesis might have shown a preference for the Ventral model over that of the Control, placing it on a continuum from Control to SS. The observed relationship between the supernormal pecking response and chick age is also not consistent with Tinbergen and Perdeck's (1950) hypothesis, because if the supernormal response was adaptive to chicks at their first feeding, it should have dwindled, rather than intensified, with age.

6.3.2 Innate feeding hypothesis

While the results presented in this thesis strongly suggest that Lesser Black-backed Gull chicks have innate feeding preferences, it is less certain that these are in any way linked to the supernormal pecking response. Thus, the hypothesis that the supernormal pecking response is an adaptation to chick feeding in early life (set out in Chapters 4 and 5), could not be substantiated. There was, however, some support for a relationship between supernormal behaviour and chick feeding. Chicks' consistent choice of striped over plain food in experiment 5.3a, and their decision to eat worms preferentially (even though discs of chicken induced the highest rate of pecking) in experiment 5.3c indicate that chicks may have innate feeding preferences for small, segmented prey of the type switched to by the adults of many species when feeding young chicks (Table 5.2). The stripes (or segments) of the foodstuffs chosen, along with their thin shape and the reddish colour of the *E. foetida* worms eaten, are also properties common to the SS. Taken together with the findings of experiments 4.2c and 4.2d, which showed that the white stripes, followed by the red colour, were the most powerful elements of the SS, these results could indeed suggest that this stimulus is effective because it taps into chicks' innate feeding preferences. Furthermore, the heightened rate of pecking seen in experiment 4.2d, where five of the six stimuli presented had at least three features of the SS, could suggest that chicks had switched from a "begging mode" into a "feeding mode", and were effectively responding to the stimuli presented as food rather than as representations of the parental bill.

Since the ability to recognize and respond swiftly to the presence of food is crucial to chick survival, particularly when competing with siblings, selection could have resulted in chicks evolving strong innate responses to any items that resemble the food items commonly delivered by adults. Such a process could have been enhanced if the food typically brought also addresses chicks' specific nutritional and energetic needs, as proposed by some authors (Spaans, 1971; Kirkham & Morris, 1979; Annett & Pierotti, 1989; Nogales *et al.*, 1995).

6.3.3 Ramachandran's hypothesis

Appealing though it might be to attribute the supernormal pecking response to an adaptation to chick feeding, many of the results described could also be interpreted in accord with Ramachandran's (2004) proposal that chicks' response to the SS is simply a non-adaptive "accident" of their neuronal wiring. However, little explicit evidence was found in support of this hypothesis, partly because the experiments were not designed to address it. Thus, the underlying mechanisms controlling the supernormal pecking response in gull chicks were not identified by this study.

6.4 FUTURE DIRECTIONS

Much of the work described in this thesis is open-ended, and thus leaves several interesting questions that could be addressed through future work. One way to approach Ramachandran's (2004) hypothesis might be to carry out a thorough investigation of supernormal pecking behaviour in representatives of a range of gull species, and perhaps other larids too. If the same kind of supernormal behaviour were to be found in all species, this would provide support for Ramachandran's (2004) assertion, indicating that there is some inherent non-adaptive property of the nervous system of these birds that brings about this atypical behaviour. However, if supernormal behaviour differs between, or is absent from, certain species, this might suggest a selective process, thus implying some adaptive role of supernormal pecking.

Further investigation of the dietary switches found in gulls would be another interesting avenue of research, which could also help to address the hypothesis that the supernormal response is an adaptation to innate feeding preferences. As discussed in Chapter 5, most of the switches described have been in large white-headed gull species with a red gonys spot (Table 5.2). However, much of the information available on chick diet has been collected using different techniques, and has concentrated on different stages of the chick period. It is also uncertain if the foods switched to by adults feeding chicks do indeed meet specific chick dietary needs. Thus, studies several gull species (including representatives from colonies with access with a variety of feeding grounds) using consistent techniques could help elucidate the exact nature of switches in early life, including whether the foods given to young chicks is adaptive, whether switches are in any way related to bill markings, and whether the foodstuffs typically delivered do indeed resemble the supernormal stimulus.

A final interesting area of research to pursue concerns the red gonys spot. As discussed, this feature acts as a signal in both parent-offspring and sexual communication (Tinbergen & Perdeck, 1950; Blount *et al.*, 2002; Kristiansen *et al.*, 2006; Pérez *et al.*, 2008; Morales *et al.*, 2009). Anecdotal observations made during fieldwork of pairs nesting in high density, open areas, where clutch size and hatching success was reduced, indicated that in addition to several birds bearing vestiges of juvenile plumage (Fig. 2.19), various individuals in these patches also had low intensity integument colouration of the legs, orbital ring and bill, and hence had diffuse, faded gonys spots (e.g. Fig. 3.12a). Given the gonys spot has already been found to convey information about more than one aspect of gull behaviour, it is possible that it operates as a general socially selected signal, of the type described in other sexually monomorphic, socially monogamous and group living animals (West-Eberhand, 1983). It could thus be worthwhile exploring whether the experimental modification of spot size and colour, similar to that employed by Morales *et al.* (2009) affects territorial behaviour in Lesser Black-backed Gulls and related species, such that species with a spot manipulated to lower its quality faced a larger number of encroachments from neighbours attempting to expand their territories, for example. Similar experiments could also investigate whether spot condition influences the stability of partnerships at the start of the breeding season, in terms of divorce rates and extra-pair mating behaviour.

Appendix I: gull species names

Current scientific name	Current English name	Alternative/previous name(s)	Described by
Creagrus furcatus	Swallow-tailed Gull	*Larus furcatus*	Neboux, 1846
Rissa tridactyla	Black-legged Kittiwake	*Larus tridactyla*, Kittiwake	Linnaeus, 1758
Rissa brevirostris	Red-legged Kittiwake	*Larus brevirostris*	Bruch, 1853
Pagophila eburnea	Ivory Gull	NA	Phipps, 1744
Xema sabini	Sabine's Gull	*Larus sabini*	Sabine, 1819
Chroicocephalus genei	Slender-billed Gull	*Larus genei*	Brème, 1839
Chroicocephalus philadelphia	Bonaparte's Gull	*Larus philadelphia*	Ord, 1815
Chroicocephalus serranus	Andean Gull	*Larus serranus*	Tschudi, 1844
Chroicocephalus maculipennis	Brown-hooded Gull	*Larus maculipennis*	Lichtenstein, 1823
Chroicocephalus bulleri	Black-billed Gull	*Larus bulleri*	Hutton, 1871
Chroicocephalus scopulinus	Red-billed Gull	*Larus (novaehollandiae) scopulinus*	Forster, 1844
Chroicocephalus novaehollandiae	Silver Gull	*Larus novaehollandiae*, Red-billed Gull	Stephens, 1826
Chroicocephalus cirrocephalus	Grey-hooded Gull	*Larus cirrocephalus*, Grey-headed Gull	Vieillot, 1818
Chroicocephalus hartlaubii	Hartlaub's Gull	*Larus hartlaubii*	Bruch, 1853
Chroicocephalus ridibundus	Black-headed Gull	*Larus ridibundus*	Linnaeus, 1766
Chroicocephalus brunnicephalus	Brown-headed Gull	*Larus brunnicephalus*, Indian Black-headed Gull	Jerdon, 1840
Chroicocephalus saundersi	Saunders's Gull	*Larus saundersi*, Chinese Black-headed Gull	Swinhoe, 1871
Hydrocoleus minutus	Little Gull	*Larus minutus*	Pallas, 1776
Rhodostethia rosea	Ross's Gull	NA	MacGillivray, 1824
Leucophaeus modestus	Grey Gull	*Larus modestus*	Tschudi, 1843
Leucophaeus scoresbii	Dolphin Gull	*Larus scoresbii*, Red-billed Gull,	Traill, 1823
Leucophaeus atricilla	Laughing Gull	*Larus atricilla*	Linnaeus, 1758
Leucophaeus pipixcan	Franklin's Gull	*Larus pipixcan*	Wagler, 1831
Leucophaeus fuliginosus	Lava Gull	*Larus fuliginosus*	Gould, 1841

Ichthyaetus melanocephalus	Mediterranean Gull	*Larus melanocephalus*	Temminck, 1820
Ichthyaetus audouinii	Audouin's Gull	*Larus audouinii*	Payraudeau, 1826
Ichthyaetus relictus	Relict Gull	*Larus relictus*	Lönnberg, 1931
Ichthyaetus leucophthalmus	White-eyed Gull	*Larus leucophthalmus*	Temminck, 1825
Ichthyaetus ichthyaetus	Great Black-headed Gull	*Larus ichthyaetus*, Pallas's Gull	Pallas, 1773
Ichthyaetus hemprichii	Sooty Gull	*Larus hemprichii*	Bruch, 1853
Larus pacificus	Pacific Gull	NA	Latham, 1802
Larus belcheri	Band-tailed Gull	Belcher's Gull	Vigors, 1829
Larus atlanticus	Olrog's Gull	NA	Olrog, 1958
Larus crassirostris	Black-tailed Gull	NA	Vieillot, 1818
Larus heermanni	Heermann's Gull	NA	Cassin, 1852
Larus canus	Common Gull	*Larus brachyrhynchus,* Mew Gull	Linnaeus, 1758
Larus delawarensis	Ring-billed Gull	NA	Ord, 1815
Larus occidentalis	Western Gull	NA	Audobon, 1839
Larus livens	Yellow-footed Gull	NA	Dwight, 1919
Larus dominicanus	Kelp Gull	Southern Black-backed Gull	Lichtenstein, 1823
Larus armenicus	Armenian Gull	NA	Buturlin, 1934
Larus marinus	Great Black-backed Gull	NA	Linnaeus, 1758
Larus michahellis	Yellow-legged Gull	*Larus cachinnans*	Naumann, 1840
Larus cachinnans	Caspian Gull	Yellow-legged Gull	Pallas, 1811
Larus argentatus	Herring Gull	NA	Pontoppidan, 1763
Larus fuscus	Lesser Black-backed Gull	NA	Linnaeus, 1758
Larus californicus	California Gull	NA	Lawrence, 1854
Larus smithsonianus	Smithsonianus	*Larus argentatus*, Herring Gull	Coues, 1862
Larus glaucescens	Glaucous-winged Gull	NA	Naumann, 1840
Larus hyperboreus	Glaucous Gull	NA	Gunnerus, 1767
Larus thayeri	Thayer's Gull	Kumlien's Gull	Brooks, 1915
Larus glaucoides	Iceland Gull	Kumlien's Gull	Meyer, 1822
Larus schistisagus	Slaty-backed Gull	NA	Stejneger, 1844

All scientific names used in this thesis follow the latest guidelines issued by the International Ornithologists' Union (2009). English names are taken from those specified on the British List, published by the British Ornithologists' Union (2009). As gull classification is in a state of flux, several of the papers referred to in this work employ English and scientific names that have subsequently changed. Where such studies are described, the species names are adjusted to be consistent with the latest guidelines. For example, references to "Herring Gulls" from North America have been altered such that the English name is "American Herring Gull", and the scientific name is "*Larus smithsonianus*" instead of "*L. argentatus*". Details of the nomenclature employed are summarized in the above table.

Appendix II: molecular sexing of gull chicks

Sexing was undertaken through extraction of DNA from faeces. This was done before chicks had been fed, and when chicks had not been in contact with other birds, so only their own DNA should have been isolated. Chicks were placed individually on a sheet of sterile laboratory paper for approximately five minutes. The faeces of those that defecated was collected with a spatula, (freshly sterilized with bleach, 70% ethanol and flame) and placed in a sterile 0.5 ml Eppendorf tube, labelled with the chick's identity. These samples were then placed in a freezer on the island until they were returned to the laboratory at Cardiff University approximately two months later, and stored at -20 °C. Unfortunately, the freezer on Flat Holm (which was also set at -20 °C) partially defrosted on more than one occasion because of problems with the island's power supply. The DNA in the faeces might have suffered some degradation as a result of this, and as such, storing the faecal matter in ethanol would probably have been more prudent.

DNA was extracted from the faecal samples of 35 chicks between 1st November 2007 and 9th March 2008, using a QIAmp DNA Stool Kit (QIAGEN Ltd, Crawley, UK) following the manufacturer's protocols. A negative control was carried out concurrently with each batch of extractions. The procedure took place in a clean fume hood in a designated laboratory that was not used for the amplification of DNA. All equipment was sterilized through autoclaving and exposure to ultraviolet light before use.

DNA was amplified for ten extracted samples in a separate laboratory using the polymerase chain reaction (PCR). The reaction mix of 20 μl consisted of 8 μl of extracted DNA, 1 μl of each primer and 10 μl of Multiplex mastermix (QIAGEN). The primers were M5/P8, a combination which was designed to amplify the DNA of nonratite birds from degraded sources (Bantock *et al.*, 2008). This produces short amplicons showing differences in intron length between the Z and W sex chromosomes at the CHD1 gene (Griffiths *et al.*, 1998; Bantock *et al.*, 2008). PCR reactions were carried out in a PerkinElmer 3100 thermocycler, with initial denaturation for 15 minutes at 95 °C, followed by 40 cycles of 30 s at 94 °C, 90 s at 52 °C, and 90 s at 72 °C, and a final extension phase of 72 °C for ten minutes. Negative controls were included in each PCR. Products were stained with ethidium bromide and separated by electrophoresis on a 2.5% agarose gel. Samples were assessed according to the presence or absence of bands: two for the female (ZW) genotype, and one for the male (ZZ) genotype. Each DNA extraction was amplified at least twice (a mean number of 4.2 amplifications, with a range of two to nine) to check for inconsistencies due to factors such as allelic dropout (whereby the female W chromosome does not appear on the gel, and therefore the individual concerned can be falsely labelled as male) or contamination (Bantock *et al.*, 2007).

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