Red-throated diver breeding ecology and nest survival on Shetland

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Candidate's declaration

I declare that the work presented in this thesis is my own and no part has been submitted for any other degree. My supervisor Dr Ruedi G. Nager has provided advice to help me develop my ideas.

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Abstract

The aim of this thesis is to identify and measure biological, environmental and behavioural factors relevant to red-throated diver breeding ecology and then to distinguish their relative importance in determining breeding success and nest survival. Migratory birds that breed at high latitudes are at particular risk from human mediated climate change because the time window available for breeding in these areas is short, and if peak abundance of key prey items alters in response to climatic cues (Shultz *et al.* 2009), it may not be possible for birds to adjust their breeding strategies to compensate. Moreover, large scale environmental cues that migratory birds use to time their migration and breeding may become less reliable (Both & Visser 2001; Frederiksen *et al.* 2007). For such species it is particularly important to understand and monitor breeding biology, particularly the factors that determine breeding performance and nest survival, as these are likely to respond to large scale ecosystem changes before population changes are detected, and additionally provide valuable information that can be used to establish conservation priorities for the species. Red-throated divers are migratory fish-eating seabirds with a predominantly arctic breeding distribution that have apparently declined in large areas of their breeding range in the recent past (Groves *et al.* 1996; Hagemeijer & Blair 1997). In addition to the demonstrated effects of food availability (Eriksson & Sundberg 1991; Ball 1994), disturbance (Pakarinen & Järvinen 1984) and vulnerability to pollutants (Eriksson & Lindberg 2005) on breeding performance, direct and indirect effects of climate change are predicted, in particular a contracting of the European breeding range (Huntley *et al.* 2006) and vulnerability to both onshore and offshore renewable energy developments (Garthe & Huppop 2004; Halley & Hopshaug 2007).This research tests the importance of proximate factors influencing red-throated diver breeding performance using modern nest survival analysis with the intention that the findings will provide clues about the larger mechanisms driving population processes. First I developed a number of linear regression models using nest temperature signatures and photographic measures of chick size that; allowed timing of breeding to be estimated from a single field visit; were of comparable accuracy to established methods such as egg flotation (Westerkov 1950); and extended the period during the breeding cycle when timing of breeding estimates could be made, to include the later stages of incubation and chick rearing. I used these techniques to obtain timing of breeding estimates for the study sample. This allowed me to use an information-theoretic modelling approach (Burnham & Anderson 2002) to determine the daily nest survival rate and evaluate the importance of a set of biological and environmental effects on red-throated diver nest survival patterns. I found support for models that suggested that nest survival increased with nest age and individual quality and decreased with laying date. I explored the effects of habitat characteristics at different spatial scales and found support for models that suggested that both environmental conditions and predator avoidance were important determinants of nest survival rate. Finally I examined nest attendance behaviour and variation in nest temperature during incubation and found patterns in attendance in relation to nest age and through the day but no strong evidence of trends in survival in relation to attendance patterns.

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Definitions and abbreviations

Throughout this thesis I use the term ‘nest survival’. This is survival of a breeding attempt from egg laying to the time when one or both chicks reach 4 weeks (see Chapter 3, section 3.3.2, *Recording nest fate,* for the reasons why I used 4 weeks to define breeding success). Stage-specific survival within this period is referred to as either egg stage and chick stage survival respectively. For consistency I have used ‘lake’ to describe all water bodies regardless of their size. Nest site refers to the nest and sometimes the area in the immediate vicinity of the nest. Breeding lake is the principal territorial unit of a breeding pair at any one time and in this study is a discrete water body occupied by a single breeding pair, providing a shoreline nest location and unless otherwise stated a location for raising offspring. The mark and recapture parameter estimation software ‘program MARK’ used for analysis of nest survival in Chapters 3 to 6 has been shortened to MARK. The estimated daily survival rate for sample nests may be referred to as DSR. Abbreviated unit measurements used are; d,days; hr,hour; km,kilometre; m,metre; cm, centimetre.

1 Introduction

The northern part of the North Sea holds large concentrations of breeding seabirds and although there has been increasing research over the past 20 years examining their breeding ecology, factors affecting breeding performance and causes of population instability (e.g. Wanless *et al*. 2005; Furness 2007), relatively little has been directed at red-throated diver populations breeding in this area. This is surprising because despite being listed on Annex 1 of the European Birds Directive and having several sites designated as Special Protection Areas for them, European populations have experienced widespread decline (Tucker & Heath 1995) and censuses of the UK population between the 1980s and 2006 (Gomersall *et al*. 1984; Gibbons *et al*. 1997; Dillon *et al*. 2009) suggest apparent instabilities in parts of the UK population. Reduced availability of marine (Ball 1994), and freshwater prey (Eriksson & Sundberg 1991); regular disturbance at breeding sites (e.g. Pakarinen & Järvinen 1984), and exposure to pollutants, in particular mercury (Eriksson *et al*. 1992) are some of the suggested reasons for these declines (Bundy 1976; Pakarinen & Järvinen 1984; Gomersall 1986). In addition to these known threats, the breeding population in Britain faces an uncertain future as a consequence of the direct and indirect effects of human-mediated climate change. Models simulating the distribution of the European population for the period 2070-2100 predict that the red-throated diver breeding range will contract north-westwards reducing in size by *ca*. 50% and as a consequence will no longer breed in Britain by the end of the 21st century (Huntley *et al*. 2006). Moreover, to limit the magnitude of climatic warming there is an urgent need to reduce CO2 emissions from fossil fuel energy production and this has resulted in proposals for renewable energy developments in core red-throated diver breeding areas, in particular on the islands of Shetland and the Outer Hebrides. At present there is little evidence-based research to assess the likely effects that these developments may have on survival, occupancy and productivity of the species.

Securing a favourable long-term conservation status for red-throated divers will need more than site protection, it requires a better understanding of the mechanisms that drive population processes so that conservation resources can be targeted toward practical measures that aim to alleviate the known and predicted vulnerabilities of the species.

1.1 Population and breeding ecology

The red-throated diver is a medium-sized, sexually size dimorphic, migratory seabird with a north holarctic and circumpolar breeding distribution between 55° and 83° N (Cramp & Simmons 1977), wintering in ice-free marine and coastal areas (Tucker & Heath 1995) where they are often found in large aggregations (Cramp & Simmons 1977; Dean *et al.* 2003; Webb *et al.* 2009). The European breeding population, excluding Greenland and European Russia, is estimated to be between 7,000 and 12,000 pairs with the largest estimates for; Norway (2,000 - 5,000); Iceland (1,000 – 2,000); UK (1,000 – 1,500); Sweden (1,000 - 1,200), and Finland (900 – 1,100) (Birdlife International 2004a). The UK population, constituting *ca.* 30-40% of the EU total, is restricted to Scotland, where it predominantly occurs in the west and north, with the populations centres on Shetland (32%); the Outer Hebrides (25%); mainland Scotland (18%); the Inner Hebrides (17%); and Orkney (8%) (Birdlife international 2004b; Dillon *et al.* 2009). In addition to the breeding population, the inshore waters of the UK have recently been identified as an important wintering area with an estimated 17,000 birds present, representing up to a third of the birds wintering in European waters (Birdlife international 2004b; O'Brian *et al.* 2008).

Globally, breeding populations are estimated to have declined. Censuses between the 1970s and 1990s report that in parts of its global range this decline has been substantial with a *ca.* 50% reduction in the number of summering birds in core Alaskan breeding areas (Groves *et al.* 1996) and 88% of the European breeding population declining by between 20 and 50% (Hagemeijer & Blair 1997). However, as the generality of these figures suggests, knowledge of population change is limited because the remoteness of breeding sites leads to infrequent and patchy monitoring. Historically the UK population declined during the 19th century and apparently recovered during most of the 20th century (Batten *et al.* 1990). As part of the first systematic national survey in 1994 a decline of 46% was identified for Shetland compared to a survey of the islands in 1983 (Gomersall *et al.* 1984; Gibbons *et al.* 1997). The most recent survey in 2006 suggested that the Shetland population was stable, but elsewhere, particularly in the Outer Hebrides, the population had increased (Dillon *et al*. 2009).

Red-throated divers typically breed at low density on shoreline or on islands of small water bodies in moorland, tundra or boreal coniferous forest within a few kilometres of fish-rich marine or lacustrine feeding sites (Batten *et al.* 1990; Tucker & Heath 1995; Hagemeijer & Blair 1997).They lay a maximum of two eggs in nests that may vary from a bare scrape in the ground to a substantial nest constructed from shoreline or floating vegetation obtained from next to the nest site. Both the laying and hatching interval between eggs is *ca.* 2 days (Bundy 1976; Dickson 1993). Incubation is largely continuous, biparental and lasts *ca.*27 days (range 24-29 days Bundy 1976; Cramp & Simmons 1977). Chicks are precocial and nidifugous, leaving the nest after *ca.* 24 hours (Cramp & Simmons 1977). Adults utilise a variety of fish prey to feed themselves and their offspring. The most common marine fish prey recorded during three breeding seasons in one North American study were; herring (*Culpeidae),* smelt (*Osmeridae)*, sea pearch (*Embiotocidae*), followed by sandeel (*Ammodytidae*) and cod (*Gadidae*) (Reimchen & Douglas 1984). Other reported marine fish prey include; sprat (*Sprattus sprattus*), goby (*Gobiidae*), stickleback (*Gasterosteus* and *Spinachia*), flounder (*Platichthys*), coalfish (*Pollachius virens*), butterfish (*Pholis gunellus*), sculpin (*Leptocottus armatus*), tomcod (*Microgadus tomcod*) and, in the arctic, polar-cod (*Boreogadus saida*) and capelin (*Mallotus villosus*). In freshwater lakes fish taken include trout and salmon (*Salmo*), char (*Salvelinus alpinus*), brook trout (*Salvelinus fontinalis*), roach (*Rutilus*), dace (*Leuciscus*), bleak (*Alburnus*), and perch (*Perca*) (Cramp & Simmons 1977). Adults provision chicks with fish, carried cross-ways in the bill, one at a time, from nearby coastal or freshwater feeding areas. The number of provisioning flights per day ranged in one study from 9 to 14 (Reimchen & Douglas 1985). Potential predators of eggs and chicks in the core Arctic breeding range include arctic fox (*Alopexla gopus*), arctic wolf (*Canus lupus*), glaucous gull (*Larus hyperboreus),* long-tailed skua (*Stercorarius marinus*), arctic skua (*Stercorarius parasiticus*) and snowy owl (*Nyctea scandiaca*) (Bergman & Derksen 1977; Dickson 1992, 1993; Eberl & Picman 1993).

On Shetland red-throated divers typically arrive in coastal areas from February onwards, visiting breeding lakes with increasing regularity from mid-March (Pennington *et al.* 2004). Eggs are laid from early May and the egg laying stage including replacement clutches extends until late July (Bundy 1976; Gomersall 1986; Natural Research unpubl. data). The earliest chicks hatch in late May or early June and fly from the breeding lake, usually to the sea, six to eight weeks after hatching (Bundy 1976; S.Hulka, D.Okill pers. obs.). Occasionally breeding pairs move young chicks overland from very small nesting lakes to adjacent larger lakes (Pennington *et al.* 2004; Natural Research unpubl. data). Breeding pairs forage for themselves and provision chicks from marine areas adjacent to breeding lakes and rarely if ever catch fish on nesting lakes (Pennington *et al.* 2004). Sandeels (*Ammodytes marinus*) are reported to be a common and favoured prey (Pennington *et al.* 2004). However during this study, other fish particularly. saithe (*Pollachius virens*) were also frequently fed to chicks, and at some sites sandeels appeared to feature rarely in chick diet (S.Hulka, pers obs.). Potential egg predators on Shetland include; hooded crow (*Corvus corone cornix*), raven (*Corvus corax*), arctic skua (*Stercorarius parasiticus*), great black-backed gull (*Larus marinus*), lesser black-backed gull (*Larus fuscus*), herring gull (*Larus argentatus*), common gull (*Larus canus*) and otter (*Lutra lutra*). Likely chick predators are great skua (*Stercorarius skua*), great-black-backed gull and otter (Bundy 1976; Gomersall 1986, J.D. Okill pers comm.). Polecat ferrets (*Mustela putorius*) are present on mainland Shetland and may also pose a threat to chicks.

1.2 Study site

The study site is located on the southern edge of the red-throated diver global breeding range and comprises a *ca.* 250 km^2 area in the central part of the island of Mainland Shetland, Scotland (60°35'N 01°25'W). Shetland is a core breeding area in the UK, has the highest density of breeding birds per km^2, and the population has been monitored more intensively than in other regions nationally (Dillon *et al.* 2009). The remote and often dispersed nature of breeding sites and the associated difficulty of obtaining an adequate sample size meant that using an area with a relatively high density of well known breeding lakes was a priority and an important reason for selecting this site. The study site comprised four core study areas that were searched to locate all breeding pairs and a supplementary sample of individual lakes outside these areas that were known from historical information to have contained breeding pairs sometime in the 10 years preceding the study (Figure 1.1). In general, the physical geography of the study site consists of peat covered hills rising to *ca.* 300m a.s.l., incised by elongated coastal inlets (Figure 1.2), and lower lying semi-improved or unimproved peat moorland with rocky outcrops in areas adjacent to the coast (Figure 1.3).The core study area as a whole was chosen to reflect the range of habitat and topography used by breeding red-throated divers on Mainland Shetland, and was delineated by the boundaries of a proposed wind farm development, roads or Ordnance Survey (OS) map gridlines.

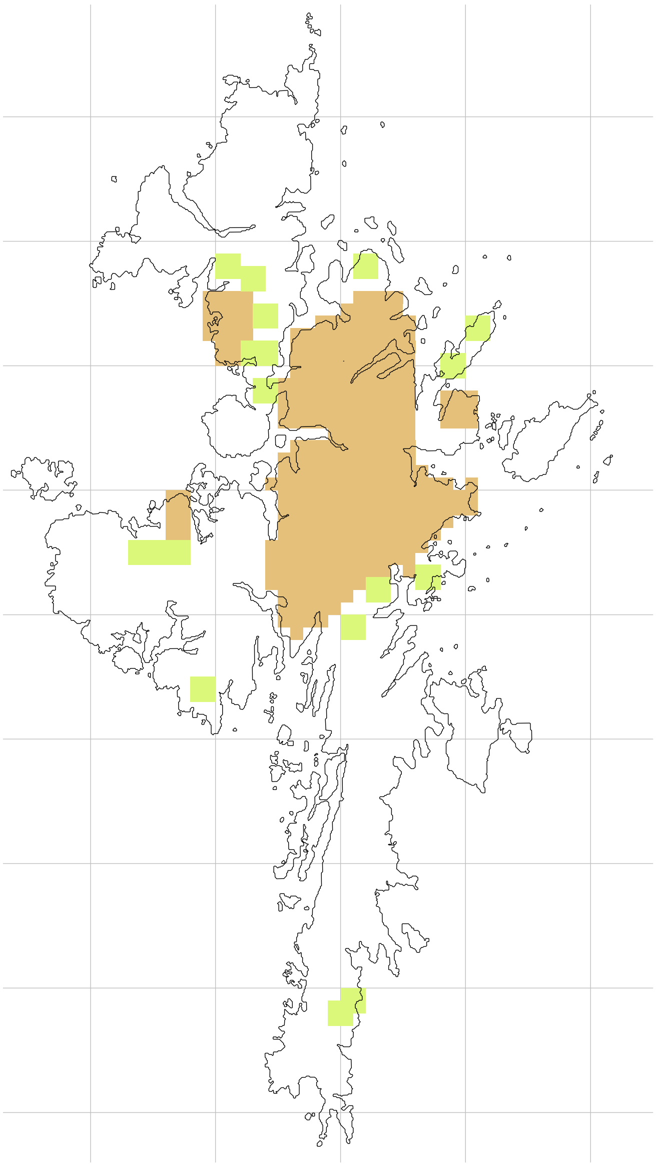


Figure 1.1 Study site, Mainland Shetland, Scotland. Four core study areas (brown) were surveyed to locate all pairs. Supplementary areas (green) containing discrete breeding sites either known from historical information or found by chance (Supplementary sites are represented within 2km bloc. Scale shown by 10km British National Grid overlay.

Figure 1.2 Typical peatland landscape in one of the core study areas.

Figure 1.3 Typical coastal landscape in one of the core study areas.

1.3 Study sample

The study sample comprised 123 widely scattered and predominantly remote breeding lakes which were studied in three breeding seasons (2006-2008). Seventy six of these were known from previous monitoring to have had at least one breeding record in the 10 years prior to the study (1995-2005, J.D.Okill;

Natural Research unpubl. data) and a further 47 were confirmed as breeding sites during initial fieldwork. Ninety three sites were in one of the four core study areas, the remaining 30 were supplementary breeding lakes outside the core areas. Study lakes ranged in size from 0.01 – 19.9 hectares (inter-quartile range; 0.1 - 0.76, mode = 0.1) and were located at an altitude of between 10 – 250m a.s.l. in either blanket peat dominated by moorland sedge (*Eriophorum* sp.), moss (*Sphagnum* sp.), or heather (*Calluna* sp.) (Roper-Lindsay & Say 1986), or in sheep grazed pasture (Figure 1.4 shows examples of nest lakes in the study sample). All nest sites were on lake shores or on the shores of lake islands (Figure 1.5 shows typical nest site locations). In the core study areas the distance between breeding lakes ranged from 0.1 - 3.4 km, the number of proven breeding pairs per 1 km by 1 km square on the Ordnance Survey map ranged from one to four pairs, and the overall average breeding density was *ca.* 0.4 pairs per km^2. No breeding lake contained more than one breeding attempt at any one time, but second breeding attempts were proven at a number of lakes after the previous attempt had failed. A first attempt was a nest with eggs or chicks discovered during a visit where all shoreline was searched and no other evidence of proven breeding was found. A second attempt was a nest with eggs or chicks discovered at a breeding lake where an attempt earlier in the same breeding season was proven and failed before the second attempt had started. Third attempts were recorded at three lakes but these were not included in the analysis. Breeding pairs foraged exclusively away from the breeding lake in adjacent marine coastal waters and were not observed taking fish from freshwater lakes (S.Hulka pers.obs.). All breeding sites were within 4.3 km of the nearest coast.

Figure 1.4 Typical red-throated diver breeding lakes

Figure 1.5 Red-throated diver nest sites

1.4 Synopsis

Nest survival estimates are an essential component of avian demographic modelling and the most effective measure for assessing avian conservation and habitat management strategies (Jehle *et al.* 2004). Recent advances in nest survival analysis (Dinsmore *et al.* 2002; Shaffer 2004) have allowed nest survival to be measured at a finer temporal scale, and rigorously tested in relation to the effects of biological, environmental, and anthropogenic factors.

I used the nest survival model in program MARK to determine daily survival rates for sample nests, and to test the effects on nest survival of factors relevant to the breeding ecology of red-throated divers. Program MARK requires that timing of breeding is known in order to calculate daily survival rates. However, this species breeds in remote locations over a protracted four month breeding period and as a consequence determining timing of breeding by observing laying or hatching during field visits is time-consuming and impractical. To resolve this, and to increase the number of sample nests that I was able to use for this study; I measured floated egg angle (Westerkov 1950); recorded nest temperature; and measured the relative size of chicks compared with adults. I used measurements from each of these techniques to construct linear regression models that allowed timing of breeding estimates to be made from field visits where laying or hatching was not observed. In Chapter 2, I describe how each model was developed and verified, and discuss their accuracy and application to nest survival studies. In Chapters 3 to 6, I examine four broad themes relevant to breeding performance in birds. I use the results of previous research in each of these areas to establish a set of hypotheses predicting effects on nest survival. These inform the building of candidate models which I use to test and distinguish the relative importance of these effects. I begin in Chapter 3 by examining the effect of variation in nest survival through the breeding cycle. Specifically, I explore the relative importance of nest age, breeding stage and year in determining nest survival rates and discuss the extent to which the results of these analyses support arguments that parental investment, individual quality, and changes in predation risk between egg and chick stages influence nest survival. In Chapter 4, I examine the influence of laying date and individual quality on breeding performance. Specifically, I explore whether red-throated diver nest survival varies with nest initiation date, the shape of this relationship and whether some attributes of individual quality contribute to it. An important aspect of individual quality is the quality of breeding sites that pairs occupy and in Chapter 5, I look at the breeding site characteristics at three spatial scales. Specifically, I attempt to determine the relative importance of environmental conditions and predation risk at nest sites and breeding lakes in determining nest survival. A result from Chapter 2 was that red-throated diver breeding attempts are particularly vulnerable to failure at the egg stage implying that incubation behaviour may be an important factor determining whether a nest survives. In Chapter 6, I examine attendance behaviour and variation in nest temperature. Specifically, I describe variation in nest attendance with nest age and through the day, and test the extent to which nest temperature and attendance patterns explain survival patterns.

2 Using nest temperature signatures and photographic measures of chick size to determine timing of breeding in species that are difficult to monitor

2.1 Abstract

Field techniques that allow timing of breeding and nest age to be estimated from a single breeding site visit are important tools for phenological and nest survival studies, particularly if the species of interest breeds in remote locations or breeding performance is likely to be compromised by repeated nest visits. I used breeding attempts where hatching date was predicted using a flotation model to assess the relative accuracy of three nest temperature signatures and two proportional adult to chick size dimensions for estimating timing of breeding in red-throated divers (*Gavia stellata*). All measures significantly predicted the hatching date estimated by flotation. The date when the nest and ambient temperature readings converged and the date when the peak mean daily nest temperature occurred were the two most accurate of the nest temperature measures predicting hatching date to an average of 2.0 days (95% CI 0.9 – 3.1) and 2.4 days (95% CI 1.6 – 3.2) respectively. Proportional chick to adult bill tip to eye distance and body length predicted hatching date to an average of 2.3 days (±95% CI 1.3 – 3.3 and 1.2 -3.4 respectively). For avian studies that have limitations on the number and timing of visits that are practical or desirable, these methods provide reasonably accurate estimates during stages of the breeding season when flotation is not possible or the later stages of incubation when it is less accurate. This allows timing of breeding to be assessed for a larger proportion of a study population, leading to more reliable and less biased estimates.

2.2 Introduction

The timing of breeding is an important life history trait in birds. It ensures that the nutritional demands of reproduction, especially chick rearing, coincide with periods of peak food availability (Lack 1968). It responds to anthropogenically induced environmental changes and can lead to a mismatch between the peak food demand of reproduction and peak food abundance with potentially negative consequences on the birds' fitness (e.g. Visser *et al.* 1998; Crick & Sparks 1999; Dawson 2007). Accurate estimates of timing of breeding are also required for analyses of nest survival (e.g. Pollock & Cornelius 1988; Bromaghin & McDonald 1993; Dinsmore *et al.* 2002; Nur *et al.* 2004), which are essential components of avian demographic modelling and the most effective method for evaluating conservation and habitat management practices (Jehle *et al.* 2004). Therefore, the ability to monitor timing of breeding in a wide range of species, especially in those which may act as bio-indicators for the wider ecosystem, has important applications. The most comprehensive long-term datasets on timing of breeding are from studies of common species where nests are readily accessible and can be monitored as frequently as necessary (e.g. Visser *et al.* 1998). However, for species that nest in remote locations, or are vulnerable to repeated disturbance, some of which may have high conservation status, multiple nest visits are not possible. In these circumstances, alternative techniques that reliably and accurately estimate timing of breeding with a minimum of disturbance are required.

Egg flotation, egg density and egg candling are the principal techniques developed to estimate timing of breeding from information obtained during a single visit to nests containing eggs. Although these techniques have been effectively used to predict timing of breeding in a wide variety of species, each has its limitations. Estimating egg density requires precise measurements of egg weight and volume which may be difficult and time consuming to achieve in the field (O'Malley & Evans 1980; Furness 1981; Lokemoen & Koford 1996; Leibezeit *et al.* 2007). Candling relies on the translucency of eggshells to see the internal contents of the egg, and is not possible for species with dark coloured or patterned eggs (Weller 1956; Lokemoen & Koford 1996). A limitation of all three techniques is the reduced accuracy in later incubation (Westerkov 1950;

Leibezeit *et al.* 2007) restricting the optimal period for assessing timing to nests found in early incubation. For species with protracted breeding seasons and nesting in remote locations, timing visits to coincide with the early incubation is often impractical. Timing of breeding can also be estimated from morphometric measures of chicks by comparing body size of sample chicks with chicks where age is known (e.g. Gilliland & Ankney 1992; Demongin *et al.* 2007). It, however, requires that birds are caught, which is often difficult for precocial species (Ricklefs 1973). There is therefore scope for other techniques which can provide predictions based on single nest visits over a less restrictive time period, or can supplement existing methods by extending the period during which predictive measures can be taken.

I assessed the predictive accuracy of two alternative techniques for determining timing of breeding in red-throated divers (*Gavia stellata*). The red-throated diver presents many of the constraints typical of species that are difficult to monitor as it breeds at remote locations and is vulnerable to disturbance (Batten *et al.* 1990; Tucker & Heath 1995). First, I monitored nest temperature fluctuations using temperature data loggers. Continuous nest temperature records have been used to identify nest survival time, nest fate and attendance patterns (Jackson & Green 2000; Arnold *et al.* 2006; Weidinger 2006; Schneider & McWilliams 2007) but have not yet been specifically tested as a tool for predicting timing of breeding. Secondly, I tested whether chick size relative to adult size measured from photographs taken of chicks swimming alongside adults during site visits can be used to predict timing of breeding. Photographs have been used to determine prey size (Larson & Craig 2006) and here I apply this to measure chick size without capture. To test the accuracy of these measures I compared them to nests of known timing of breeding.

2.3 Methods

I studied red-throated divers nesting at 123 widely scattered lakes, in a 250 km^2 area of central Mainland Shetland, Scotland (60°35'N 01°25'W) during three breeding seasons (2006-8). Breeding sites received an initial visit between late May and mid June when the majority of pairs on Shetland are incubating (Bundy 1976; Gomersall 1986). At sites where the first visit did not confirm an active breeding attempt, sites were visited at least once more before the end of July to detect late attempts. Breeding attempts initiated after this time are very unlikely.

I made a single visit to active nests during incubation to float eggs and install temperature loggers (see below). During the chick stage between mid June and late August I re-checked all active breeding sites at least once to record the presence and absence of chicks and took photographs of any chicks present alongside a parent bird (see below). Chicks grow to full size by four weeks and after that chick mortality is uncommon (Bundy 1976). Hence, breeding attempts with at least one chick four or more weeks after hatching were considered to be successful. I compared breeding success between nests with no nest visit and nests where loggers were installed and eggs floated.

2.3.1 Timing of breeding

Occasionally nest visits coincided with hatching and hence timing of breeding of those nests is known. In order to achieve a good sample size of known-aged breeding attempts I supplemented this sample with nests where I floated the eggs; a technique shown to work well with this species during early incubation (Rizzolo & Schmutz 2007). I floated eggs by placing them in a clear plastic container filled with water. Due to the air cell forming at a constant rate in the blunt end of a developing egg, the egg will position itself predictably in the water column when immersed under water. I photographed the egg's position in the water column using a digital stills camera and stored images in 'jpeg' format. From the photographs, I first assigned eggs to float categories used in a previous study on red-throated divers by visually inspecting the images (Rizzolo & Schmutz 2007). To determine the exact float angle I used the dimensioning function in AutoCAD® (Autodesk Ltd, Farnborough, Hampshire, UK) to measure the angle between the base of the container and the long axis of the egg from the uploaded digital photograph (Figure 2.1). Normally, only the blunt end of the egg rises up and the rest of the egg stays in contact with the bottom of the container (hereafter referred to as *unsuspended* eggs). For eggs that were suspended in the water column I also measured the maximum exposed diameter and exposed height above the water surface. Each egg was floated twice to evaluate measurement error in the flotation technique. Mean flotation angle from the two measurements per egg were taken and only one value per breeding attempt per year was used in all subsequent analyses.

From nests where the hatching date was known to within 2-3 days and eggs had also been floated (*N* = 11 nests) I constructed the reference flotation model. I observed three nests that hatched on the day of observation (hatching in progress, part hatched clutch with a small chick in the nest, chick with wet down in the nest) and eight breeding attempts with chicks less than 30% of their parent's body size as measured from photographs assumed to have hatched two days before the nest visit (see section 2.3.3, *Relative chick size models* - for how chick size was measured). Chicks whose hatching date was precisely known reached 30% of their parent's body size at an age of 2-3 days (S. Hulka unpubl. data). Photographs included in the reference flotation model were excluded from the relative chick size models. Where I was able to associate a specific egg with the hatching date for that egg I used that egg's float angle (*N* = 3), otherwise I used the mean angle per clutch (*N* = 8).

2.3.2 Nest temperature models

Nest temperature records should be able to reveal hatching date relatively accurately as eggs are more or less continuously covered by either of the parents and chicks leave the nest within 24 hours of hatching; incubation takes on average 27 days (range 24-29 days; Bundy 1976; Cramp & Simmons 1977). Brooding of young on the nest or elsewhere along the shoreline can continue for more than a week after hatching and is characterized by frequent recesses of the parent (Natural Research unpubl. data). Nest temperature was recorded at randomly selected nests that were discovered either before laying or while incubating during 2007 and 2008. I securely housed iButton® thermal data loggers (Model: DS 1922 L-F5 Thermochron: Maxim/Dallas Semiconductor Corp., Sunnyvale, CA) at one end of a 70mm long plastic tube. I covered the uppermost surface with a piece of black polyester gauze. To install loggers I briefly removed eggs and pushed the plastic tube containing the logger with the recording surface uppermost into the ground (usually soft peat) in the centre of the nest until it was flush with the nest base. Installing a logger took approximately one minute. The logger was typically located underneath the eggs, and completely covered by a sitting bird. Initially in 2007 I recorded a temperature every six minutes which allowed for a maximum of 33 days of recording. Recalculating nest temperature records only using every second temperature reading (i.e. every 12 minutes) gave the same results for estimated hatching date as using a 6-minute recording interval (analyses not shown). In 2008 I therefore set loggers to record temperature every 12 minutes allowing to record for 66 days and increasing the chances of recording of the complete incubation period at nests where loggers were installed before laying. The loggers were left in situ until after the chicks had left the nest for up to 10 weeks. In all analyses I used the 12-minute recording interval.

Each year throughout the breeding season I also recorded ambient temperature using iButtons that were housed and covered in the same way as nest loggers, pushed in the ground until flush with the ground surface. They were set at the same recording interval as the nest-installed loggers. To reflect the geographic variation within the study area ambient loggers were located at three sites and were installed in similar locations and within comparable vegetation to actual nest sites. In the analysis I used the ambient logger located closest to each nest to compare nest and ambient temperatures.

I assumed that specific events around the time of hatching corresponded to identifiable signatures on the nest temperature records and these can be used to estimate hatching date. Specifically, I predict that:

1. A newly hatched chick in the nest generates the highest mean temperature on that day around hatching so that the day of hatching corresponds with the *peak mean daily temperature*.

2. Increased frequency of parental recesses during the 1-2 days after hatching when the chicks are brooded on the nest results in a *maximum daily variation in temperature*.

3. Cessation of nest use after hatching results in the *convergence of nest and ambient temperature*.

To estimate (1) and (2) I calculated average temperature and standard deviation in temperature during each 24-hour period (midnight to midnight) for each nest and used the date of the highest mean and standard deviation in daily temperature, respectively, as estimates of hatching date. To estimate (3) I determined the point at which the nest and synchronously recorded ambient temperatures converged. By comparing the mean differences in daily mean temperatures for pairs of synchronously recording ambient loggers I found that the range of the mean difference ± 2 standard errors was 3°C, and hence nests over 3°C warmer than ambient were assumed to be attended by parents. I then calculated the difference between daily mean nest and corresponding ambient temperatures and I took the earliest date with a difference less than 3°C as an estimate of hatching date.

2.3.3 Relative chick size models

I measured chick size relative to their parent's size by photographing a chick alongside one of its parents when they were swimming < 5m apart with their lateral profile fully side on to the camera. Photographs were taken using a 5 megapixel digital stills camera with a 12x or 18x zoom and stored in 'jpeg' format. A suitable photograph took on average approximately five minutes to obtain. From these photographs I obtained bill and body size for adult and chick using AutoCAD®. Body length was the distance between the tip of the tail and the front of the breast along the waterline and bill length the distance between the bill tip to the centre of the eye. I divided the size of the chick by the size of the adult to obtain a relative measure of chick size (Figure 2.2). Only one measurement was used for analyses per breeding attempt per year.

2.3.4 Statistical analysis

The statistical analysis was carried out using SPSS (SPSS Inc. version 15). For all statistical analyses, tests were two-tailed with the significance level set at $P = 0.05$ and given are mean and the 95% confidence intervals. Data were checked for the assumptions of parametric tests and where necessary appropriate transformations were carried out. I used linear regressions with the age-estimator regressed on age (Dapson 1980). First, I constructed the reference flotation model using the floated eggs from breeding attempts with observed hatching date. I then used the mean egg angle of a clutch and the reference flotation model to determine hatching dates for a larger sample of nests and compared their hatching dates with the estimates of hatching date obtained from relative chick size and nest temperature. For temperature records I regressed the estimated hatching dates against the dates calculated from the reference flotation model. For chick size I regressed relative bill and body length on the number of days after hatching. To assess the accuracy of these methods I calculated the 95% confidence limits of hatching dates for a given float angle, nest temperature or relative chick size using the equation for individual predictions (i.e. $m = 1$) (Zar, 1984, equation 17.29, p 275).

2.4 Results

Using all monitored sites where a breeding outcome was known ($N = 241$) the average number of at least four weeks old young per breeding attempt was 0.58 (SE = 0.05) and an average of 42% of attempts raised at least one chick to four weeks or more. There was no difference in nesting success between breeding attempts that received a single nest visit to float eggs or install loggers and those with no nest visit ($\chi^2_1 = 1.02$, $P = 0.36$).

Measurement of flotation angle in unsuspended eggs was highly repeatable ($r = 0.99$, $P < 0.001$, $N = 135$ eggs from 83 nests). In a further 15 nests I measured the angle on suspended eggs and the measurement of float angle was less repeatable ($r = 0.54$, $P = 0.02$, $N = 20$ eggs from 15 nests). Assigning egg float angles to the flotation categories described by Rizzolo and Schmutz (2007) gave very similar hatching dates to the known hatching date ($F_{1,9} = 42.47$, $P < 0.001$, $R^2_{ad\,j} = 0.81$) with an average difference between observed and estimated hatching dates of 2.4 days (95% CI: 1.0 – 3.8 d). Using the exact float angle of unsuspended eggs gave a similar result ($F_{1,7} = 37.18$, $P < 0.001$, $R^2_{adj} = 0.82$, excluding two breeding attempts where eggs were suspended in the water column; Figure 2.3) with a lower average difference between observed and estimated hatching dates of 1.6 days (95% CI: 0.5 – 2.7 d). I therefore used the regression equation based on exact float angles of unsuspended eggs for the reference flotation model.

I had nest temperature data for 17 breeding attempts with hatching date known from egg flotation. Mean daily nest temperature was 23.8°C (SE = 0.47, $N = 17$) and the corresponding mean ambient temperature was 12.8°C (SE = 0.31, $N = 17$). Figure 2.4 shows an example of a nest and ambient temperature record for one breeding site. Of the three nest temperature indices the convergence of nest and ambient temperature was the most accurate predictor of hatching date (Table 2.1) with an average residual error of 2.0 d (95% CI = 0.9 – 3.1 d; Figure 2.5a). In this model I excluded a single outlier which strongly influenced the model (Cook's distance > 1; outlier included: $\log_{10}y = 1.92 + 0.002x$). The convergence of nest and ambient temperature systematically overestimated hatching date compared to egg flotation by *ca.* 2 days (2.1 d, SE = 0.74), $t_{15} = 2.89$, $P = 0.01$). Hatching date estimated by the peak mean daily nest temperature gave a similar result with an average residual error of 2.4 days (95% CI = 1.6 – 3.2 d; Figure 2.5b). The date of the peak mean daily temperature estimated a hatching date that was significantly earlier than expected from the reference flotation model (-3.6 d, SE = 0.84, $t_{16} = 4.08$, $P = 0.001$). The maximum daily variation in temperature was the least accurate of the three nest temperature measures with an average residual error of 4.2 days (95% CI = 2.2 – 6.2 d; Figure 2.5c). Averaging hatching dates from the peak temperature and the convergence of nest and ambient temperature gave estimates that were more accurate than either individual model with an average residual error of 1.4 days (95% CI = 0.8 – 2.0 d; Figure 2.5d) and no difference to the hatching date estimated from the flotation (-0.4 d, SE = 0.45, $t_{15} = 0.96$, $P = 0.35$).

Relative chick body size was determined from photographs taken at 15 breeding attempts where the eggs were also floated. Relative bill length could only be measured for 11 of these because bill profiles in 4 attempts were not fully side on to the camera when the photograph was taken. The proportional difference in bill length and body length between individual pair members, photographed when they were < 5m apart with their lateral profile fully side on to the camera, was on average 8.1% (SE = 0.02; $N = 9$ pairs) and 8.2% (SE = 0.02, $N = 9$ pairs), respectively. The proportional difference in bill length and body length for pairs of siblings photographed together was 4.6% (SE = 0.03, $N = 4$ pairs) and 7.1% (SE = 0.02, $N = 10$ pairs), respectively.

Relative chick bill length and body length were related to the number of days elapsed since the hatching date (Figure 2.6, Table 2.1) with an residual error of 2.3 days (95% CI = 1.3 – 3.3 d; Figure 2.6a) for the bill length model and 2.3 days (95% CI = 1.2 – 3.4 d; Figure 2.6b) for the body length model.

There were six nests with hatching date known from egg flotation where relative chick body size and nest temperature were recorded. Hatching dates predicted by the convergence of nest and ambient temperature and the peak mean daily nest temperature were closest to the hatching date based on egg flotation (average residual errors were 1.0 d (95% CI = 0.4 – 1.6 d) and 1.3 d (95% CI = 0.5 – 2.1 d). Relative chick bill and body length yielded similar results as the main dataset with slightly higher average residual errors than nest temperatures; 2.1 days (95% CI = 0.9 – 3.3 d) and 1.8 days (95% CI = 0.7 – 2.9 d), respectively. As in the main dataset maximum daily variation in temperature had the largest residual error of 3.4 days (95% CI = 0.8 – 6.0 d).

Table 2.1 Regression analyses and accuracy for (a) three nest temperature measures and (b) two chick size measures. ($P < 0.001$ for all regression models).

Model	*df*	F	R^2_{adj}	Linear regression	$\bar{y} \pm$ SE
(a) Nest temperature models					
Convergence between nest and ambient temperature	1,14*	145.38	0.91	$\log_{10}y = 1.83 + 0.002x$	2.3 ± 0.007**
Peak mean daily nest temperature	1,15	150.36	0.90	$\log_{10}y = 1.91 + 0.002x$	2.3 ± 0.007**
Maximum mean daily variation in nest temperature	1,15	27.57	0.62	$\log_{10}y = 2.01 + 0.001x$	2.3 ± 0.014**
Peak main daily and convergence between nest and ambient nest temperature averaged	1,14	368.10	0.96	$\log_{10}y = 1.85 + 0.002x$	2.3 ± 0.005**
(b) Relative chick size models					
Bill length	1,9	144.10	0.94	$y = -30.61 + 84.19x$	20.5 ± 2.95
Body length	1,13	138.05	0.91	$y = -26.04 + 68.22x$	21.2 ± 3.25

* single outlier removed (see main text) ** Estimates of the dependent variable are $\log_{10}$-transformed

Figure 2.1 Measuring exact angle of unsuspended and suspended red-throated diver eggs using the flotation method.

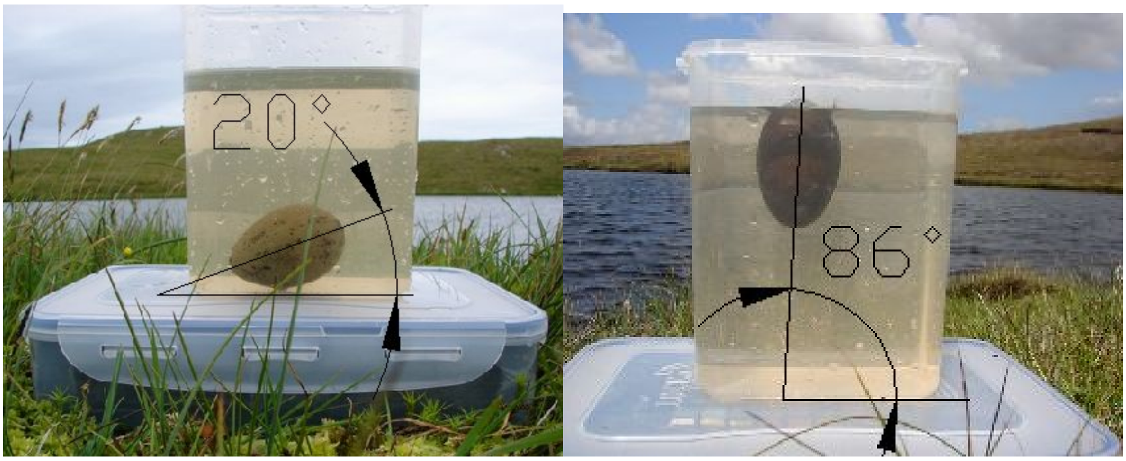
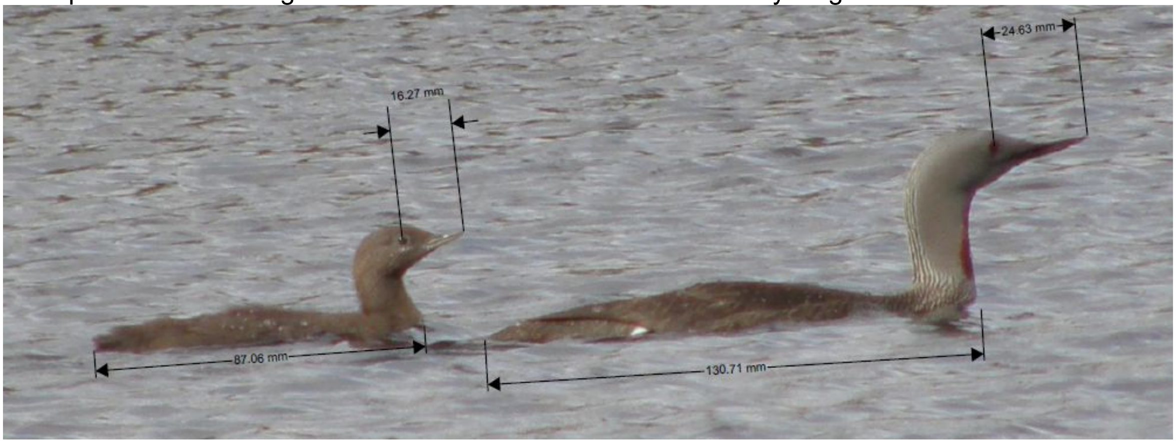


Figure 2.2 Measuring red-throated diver relative chick to adult size from photographs. In this example relative bill length is 16.27/24.63 = 0.66 and relative body length = 87.06 x 130.71 = 0.67



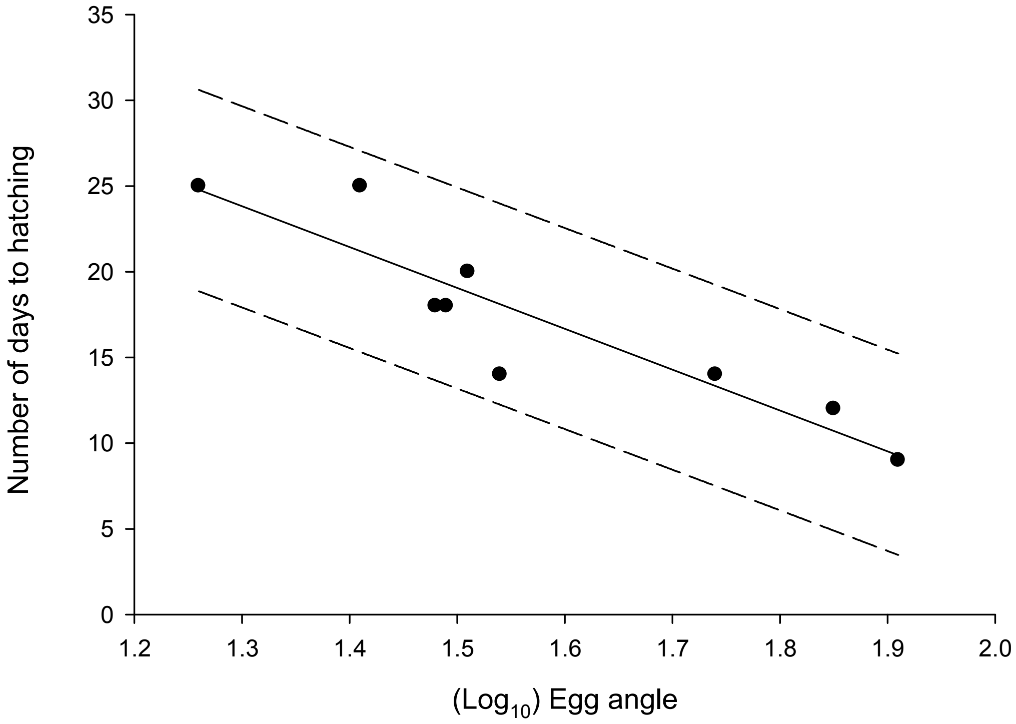


Figure 2.3 Relationship between the unsuspended egg angle and the number of days before the observed hatching date. The linear regression equation $y = 54.56 - 23.68 \text{Log}_{10}x$ describes the 'reference flotation model' that was used to obtain a measure of hatching date for breeding attempts where eggs were floated. The dotted lines represent the upper and lower 95% confidence limits for individual predictions.

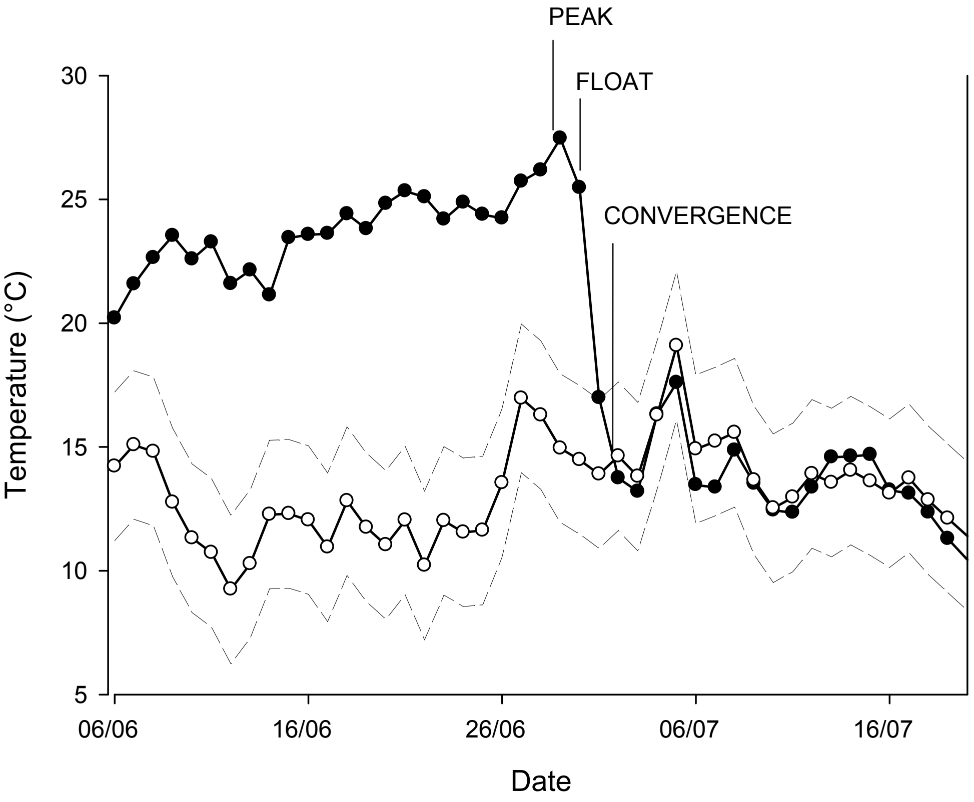
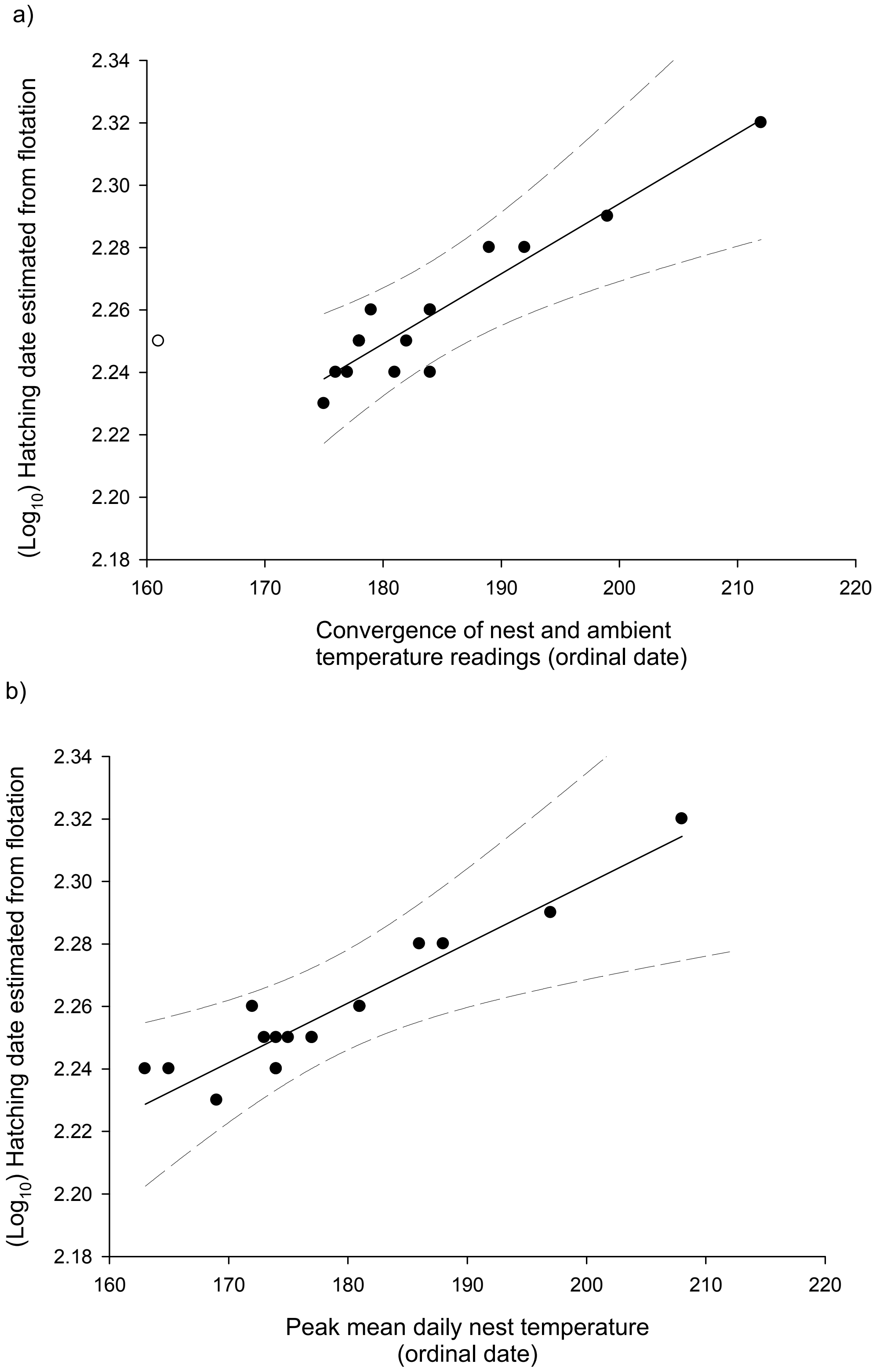
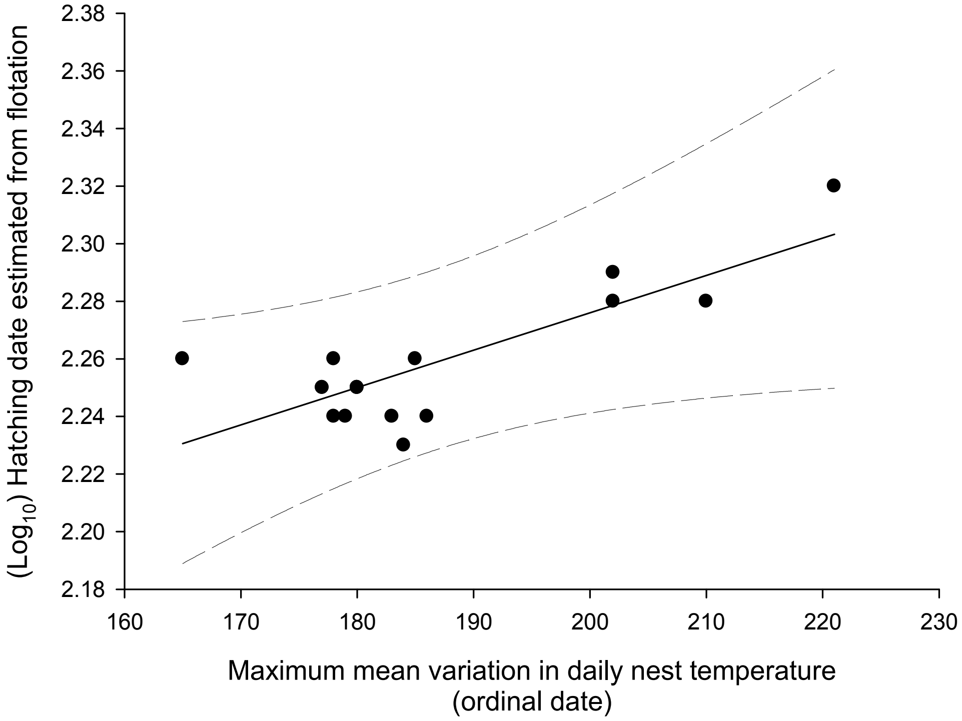


Figure 2.4 An example of a nest and ambient temperature record from 2008 showing mean daily nest temperatures for one nest (solid circles), and mean daily ambient temperature for the same period (open circles). The ±3°C limits around the mean daily ambient temperature (dashed lines) is used to determine the date of convergence between nest and ambient temperatures. FLOAT = hatching date based on egg flotation; PEAK = hatching date predicted by the peak mean daily nest temperature model; CONVERGENCE = hatching date predicted by the convergence of nest and ambient temperature model.

Figure 2.5 Relationship between hatching dates predicted by the reference flotation model and (a) the date of convergence between nest installed and ambient logger traces with a single outlier (unfilled circle, see text) (b) the date of the peak mean daily nest temperature (c) the date of the maximum mean daily variation in nest temperature. (d) the average date between the convergence model (excluding outlier) and the peak mean daily temperature model. The dashed lines represent the upper and lower 95% confidence limits for individual predictions.



c)


(Log$_{10}$) Hatching date estimated from flotation
2.38
2.36
2.34
2.32
2.30
2.28
2.26
2.24
2.22
2.20
2.18
160
170
180
190
200
210
220
230
Maximum mean variation in daily nest temperature (ordinal date)

d)

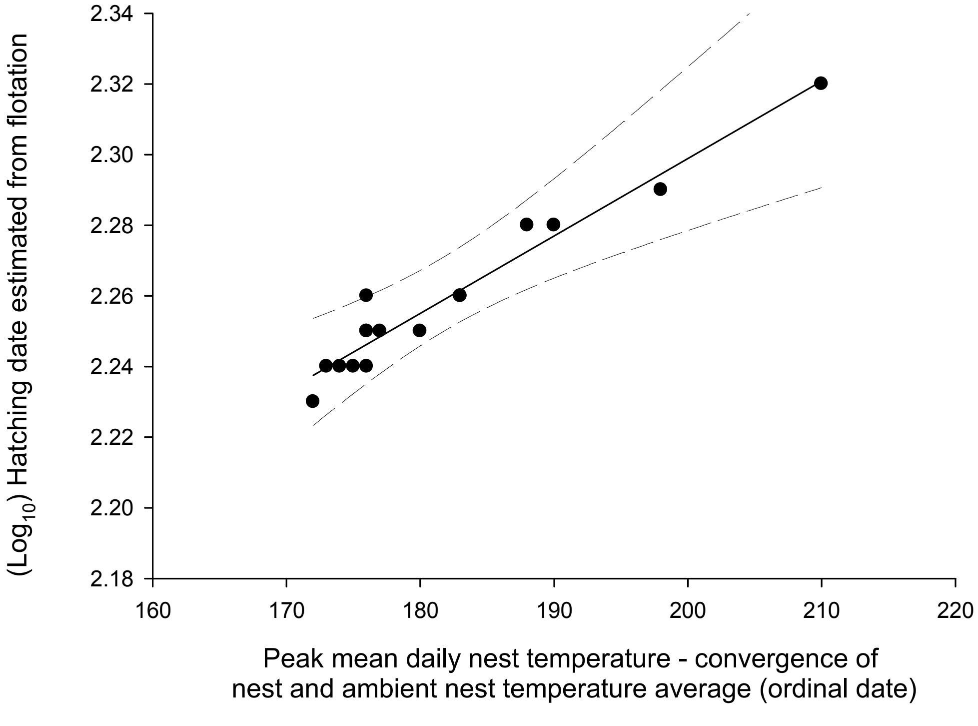
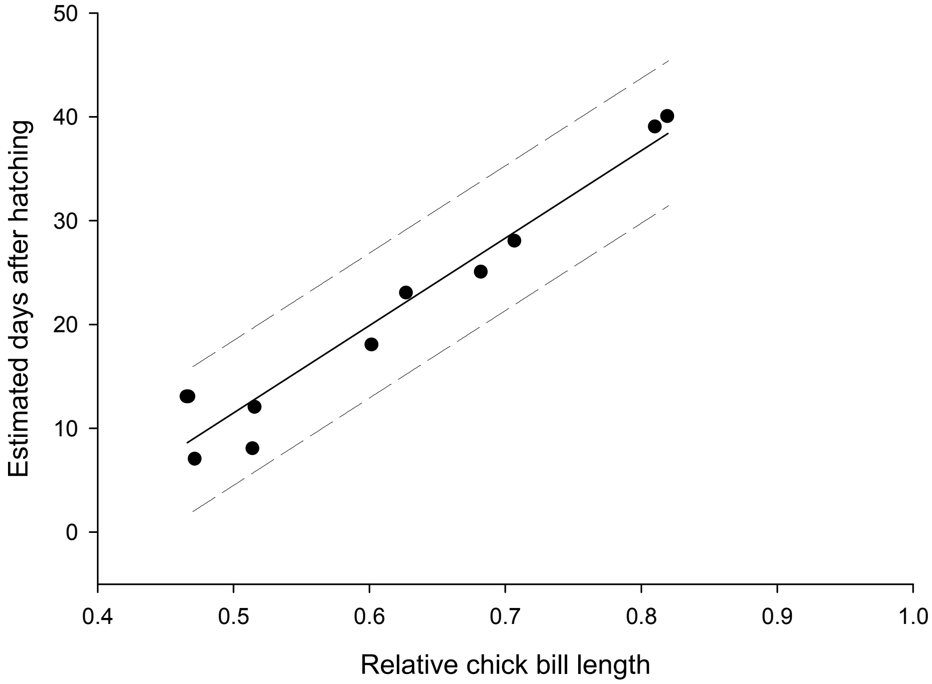
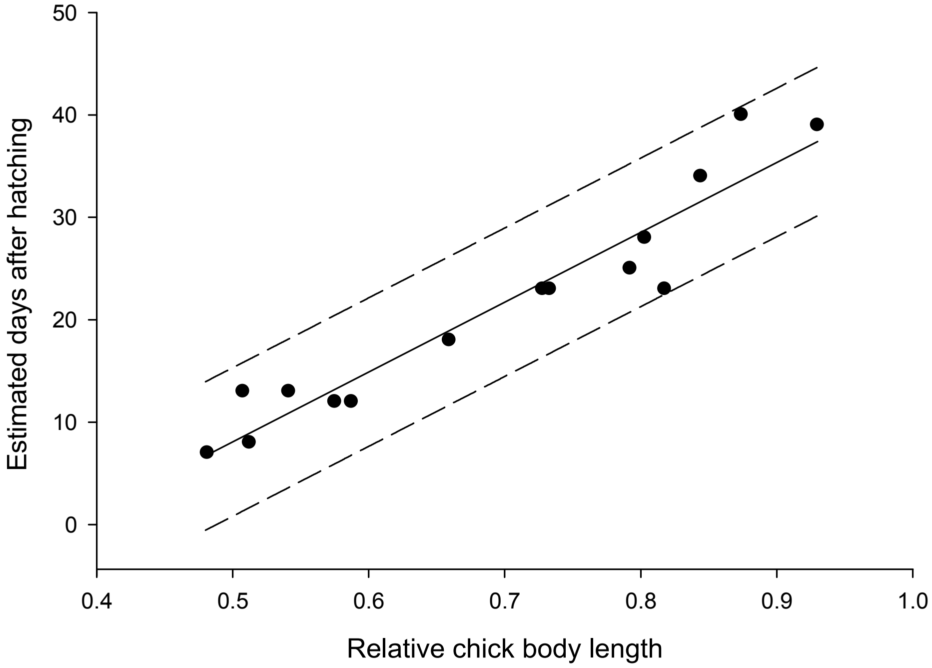

(Log$_{10}$) Hatching date estimated from flotation
2.34
2.32
2.30
2.28
2.26
2.24
2.22
2.20
2.18
160
170
180
190
200
210
220
Peak mean daily nest temperature - convergence of nest and ambient nest temperature average (ordinal date)

Figure 2.6 Relationship between hatching dates predicted by the reference flotation model and (a) relative chick bill length (b) relative chick body length (relative chick size is chick size divided by adult size, see Methods). The dashed lines represent the upper and lower 95% confidence limits for individual predictions.

a)



b)



2.5 Discussion

Egg flotation provided a good estimate of hatching date allowing for a valid comparison with estimates of the timing of breeding based on relative chick size and nest temperature. Obtaining the exact egg angles of eggs not suspended in the water column shows a close relationship with time until hatching, and resulted in more accurate estimates than using float categories determined by Rizzolo and Schmutz (2007). The use of simple float categories had been previously suggested because they are quick to assess, but they may not make full use of this relationship. The setting up, floating and photographing of a full clutch of two eggs took approximately 5 minutes per nest and is likely to be comparable with the time taken to assign float categories by eye. Measuring the exact float angle also has the advantage of being more objective because float angle for all eggs can be retrospectively measured by a single observer away from the field situation. Furthermore, for long-term studies on the timing of breeding the use of photographs allows comparison of data across years. Once eggs become suspended in the water column, however, there is no longer a good prediction of hatching date. Across a variety of species, eggs remain unsuspended for between 40 to 70% of the total incubation length (estimated from data in Hays & LeCroy 1971; van Paassen *et al*. 1984; Leibezeit *et al*. 2007; Rizzolo & Schmutz 2007; Rush *et al*. 2007). To ensure reliable estimates of timing of breeding fieldworkers need to visit potential nest sites at intervals that correspond with the unsuspended egg phase. For red-throated divers, eggs remain unsuspended for 65% of the total incubation period. Hence a field visit every 18 days is required, but for species with shorter incubation periods nest visits need to be more frequent (see Sandercock 1998).

2.5.1 Continuous nest temperature records

Continuous nest temperature records can be used to estimate timing of breeding. The three individual measures derived from nest temperature records have different merits and weaknesses in determining timing of breeding in red-throated divers. The date when nest and ambient temperature converged and the date of the peak mean daily temperature were the most accurate predictors of hatching date, but not the date when daily variation in nest temperature was maximal.

The convergence between nest and ambient temperature is likely to predict hatching date in nests where chicks typically leave the nest very soon after hatching and there is no protracted post-hatching brooding at the nest. In the case of the red-throated diver the convergence model provided a good estimate of hatching date, but it systematically overestimated hatching date compared to egg flotation. This is most likely because newly hatched red-throated diver chicks are intermittently brooded at the nest for the first 1 – 2 days (S. Hulka pers. obs.), and hence this delays the convergence of nest and ambient temperature until after the chicks left the nest permanently. This method is likely to work well for species nesting in regions where ambient is typically different from nest temperature. However, I observed one case where nest temperature during an unusually long incubation recess coincided with warm weather resulting in a temporary convergence between ambient and nest temperature. Pre-hatching nest temperature patterns are easily distinguished from post-hatching records (see Figure 2.4) and therefore a visual check of temperature traces can safeguard against this type of error.

Mean daily nest temperature may peak at hatching because of higher egg temperature late in incubation (Caldwell & Cornwell 1975; Wilson & Verbeek 1995; Poussart *et al.* 2000) and/or because brooded chicks lie directly on the logger. In red-throated diver, nest temperature was higher at the end of incubation compared with mid incubation (S. Hulka et. al. in prep.). A brood of red-throated diver hatches over *ca.* 1.6 days (Dickson 1993) and hence taking the mean egg angle per clutch may estimate a slightly later date than when the first egg hatches. The date of the peak mean daily temperature estimated a hatching date that was 3.6 days earlier than expected from the reference flotation model, which is more than one would expect simply from the hatching spread in a brood. This suggests that the nest temperature peaks before the first egg hatches. A regression using the average of the peak nest temperature and the convergence of nest and ambient temperature indices predicted hatching dates closest of all the test models to the reference flotation model. I recommend this approach wherever possible as a robust alternative when flotation is not possible. Finally, intermittent brooding after hatching was also expected to increase temperature variability. However, the high frequency of intermittent brooding resulted in a relatively weak effect on temperature variability and this measure did not provide a reliable estimate of timing of breeding in red-throated divers.

This corroborates the effectiveness of temperature loggers for remotely monitoring aspects of breeding behaviour of wild birds (Hartman & Oring 2006; Ardia *et al.* 2009), where there is little ambiguity between incubation and post-hatching temperature readings from the nest. The relatively low cost of iButtons allows whole study populations to be monitored simultaneously providing a valuable tool for phenological and nest survival studies.

2.5.2 Relative chick size

Relative chick size derived from photographs can also be reliably used to estimate hatching date in red-throated divers. The proportional difference in bill length between the pair members photographed together in profile was similar to the observed within-pair difference in culmen length derived from morphometric data in Okill et al. (1989) suggesting that measurement error of the photographic method was relatively small.

A likely source of variation in my relative chick size measurements was that I could not allow for sexual size dimorphism in the parents or variation due to age differences between siblings. The accuracy in determining hatching date in sexually size-monomorphic species may be therefore better than I found in this study. This type of error could be minimised by using traits that vary least between sexes. A study on red-throated divers from Shetland and continental Europe found that sexual dimorphism in body weight was 15% whereas it was only 5% in culmen length (based on figures in Okill *et al.* 1989). Attempts to increase the accuracy of the relative chick size measure should also consider potential within-season variation in adult size (see van de Pol *et al.* 2009). A limitation of the relative chick size technique is that it only uses information from breeding attempts that reached the chick-rearing stage and therefore should not be used on its own to quantify timing of breeding.

Estimating timing of breeding is of increasing interest for detecting responses of species to macro-environmental change and an essential component of modern nest survival analyses. Measuring the angle of floated eggs is a powerful technique for achieving this, but it has only a restricted time window in which it works effectively. This limitation is particularly relevant when the number of nest visits is restricted by the remoteness of breeding sites or the vulnerability to disturbance of the study species. Some nests may only be discovered at the chick rearing stage whereas others may have been visited when a nest but no eggs are present and subsequent visits are not possible until much later. In these circumstances an integrated approach, employing a range of calibrated measures with similar accuracy that predict timing of breeding using data from different stages of the breeding cycle would permit a less restrictive visit strategy and study populations to be sampled more widely. Where nesting attempts are discovered as part of an unbiased sampling strategy, an approach using several validated techniques with similar accuracies can allow phenological information to be effectively collected as part of census or productivity monitoring programmes.

3 Variation in red-throated diver nest survival through the breeding cycle

3.1 Abstract

Models based on optimal parental investment predict an increase in nest defence as incubation progresses leading to an increase in survival with nest age. This effect however could also be due to early nest loss by lower quality pairs, leaving higher quality pairs with more resources available for nest defence. Alternatively nest survival may be largely influenced by a shift in predation risk as a consequence of changes in parental care behaviour between the egg and chick stage. Here I use a modelling approach to evaluate the effect of these factors on nest survival in red-throated divers. Nest survival through the breeding cycle was not constant and was best described by a linear effect of nest age. Daily nest survival for the best supported model followed an increasing trend from the start of the incubation and was highest and most stable during the chick stage. Overall daily survival rate (DSR) using an intercept only model was higher for the chick stage compared with the egg stage and significantly higher for first compared to second attempts. Variation in nest survival of red-throated diver through the breeding cycle appears to be either function of increasing parental effort as the breeding season progresses or due to selective mortality of nests from poorer quality birds.

3.2 Introduction

Nest survival estimates are an essential component of avian demographic modelling and the most effective measure for assessing avian conservation and habitat management strategies (Jehle *et al*. 2004). These estimates are particularly valuable if the species breed in fragile or threatened habitats, are of high conservation status or are monitored infrequently because of their remote breeding location. Modern nest survival techniques allow variation in nest survival between censuses and within breeding seasons to be estimated and biological, environmental and anthropogenic variables underlying nest survival trends to be thoroughly investigated. It thus provides a valuable tool for monitoring a species' conservation requirements.

The importance of obtaining accurate and reliable nest survival measures is reflected in numerous estimators developed since the 1960's (reviewed in Jehle *et al.* 2004). Most of these methods, and as a consequence the majority of nest survival studies, have been based on the Mayfield estimator (Mayfield 1975). Despite its widespread use, the technique is limited because 1) it assumes that survival is constant throughout the study, 2) the timing of losses must be exactly known and 3) it is not able to assess the effects of covariates on nest survival rates (Dinsmore & Dinsmore 2007). For many species, the probability of nest predation may vary in relation to one or more time-specific variables, such as nest age or nest initiation date. To investigate variation in nest survival, Mayfield estimates are often averaged for different stages of the breeding cycle or for arbitrary periods within each stage (Grant *et al.* 2005). For remotely nesting or vulnerable species, determining the timing of breeding losses is likely to require nest visit frequencies that are either impractical or substantially increase the risk of nest failure. Recent advances in nest survival modelling (Dinsmore *et al.* 2002; Shaffer 2004) have overcome these limitations, allowing nest survival to be examined at a finer temporal scale and the effects of relevant covariates to be tested.

Models based on optimal parental investment predict an increase in nest defence as incubation progresses leading to an increase in survival with nest age. This may be due to increasing parental effort and diminishing possibility of renesting (Knight & Temple 1986; Montgomerie & Weatherhead 1988; Redondo 1989; Westneat 1989; Brunton 1990) and/or early nest loss by lower quality pairs, leaving higher quality pairs that have more resources available for nest defence. This combined with a positive correlation between the intensity of nest defence and breeding success (e.g. Greig-Smith 1980; Blancher & Robertson 1982; Byrkjedal 1987) suggests that nest survival is likely to improve as the breeding cycle progresses. These effects may differ according to the specific breeding biology of a species. For example, in altricial species nest survival through the egg, and most of the dependant nestling stage will be to some extent a function of increasing levels of nest defence reflecting increasing parental investment and continuing dependence of the young, whereas in precocial species nest survival rate may change soon after hatching when the young leave the nest and relate to diminishing parental care and the effect of different survival pressures compared with the egg stage (Montgomerie & Weatherhead 1988).

The red-throated diver (*Gavia stellata)* is a remote nesting, infrequently and non-intensively monitored seabird (e.g. Gomersall 1986; Gibbons *et al*. 1997; Dillon *et al*. 2009) with a demonstrated vulnerability to changes in prey availability (Eriksson & Sundberg 1991; Ball 1994), pollutants (Eriksson *et al*. 1992), and regular disturbance (Pakarinen & Järvinen 1984). Previous studies have concluded that the principal proximate cause of breeding failure in red-throated diver is avian or mammalian predation with other factors such as the flooding of nests, infertile or addled eggs being less important (Bundy 1976; (Bergman & Derksen 1977; Gomersall 1986; Dickson 1993; Eberl & Picman 1993; Dahlén & Eriksson 2002). Four of these studies (Bundy 1976; Gomersall 1986 on Shetland; Dickson 1993; Eberl & Picman 1993 in North America) have compared egg and chick stage failure rates. All found that failure at the egg stage was higher than at the chick stage, although both Gomersall (1986) and Dickson (1993) recorded higher chick mortality for one of their study years. Two of these studies assessed variation in survival within the egg stage. Eberl and Picman (1993) found that nests had the highest failure rate in the first seven days of incubation. Dickson (1993) found that average egg mortality rate increased as incubation progressed and peaked in the final week of incubation, however nests were visited repeatedly and it is possible that the increased mortality was a cumulative effect of repeated disturbance rather than a feature of the breeding ecology. Any effects of disturbance were not reported. Survival patterns within the chick stage appear less ambiguous. All four of the published studies above indicate that most chick mortality occurs during the first three weeks after hatching. Of the two studies that examined this stage in some detail, Gomersall (1986) found that a third of all breeding attempts in one study year failed during the first 10 days after hatching, and Dickson (1993) found that mortality was greatest in the first week after hatching and decreased in each of the subsequent three weeks.

These results suggest that both nest age and stage specific trends may exist in red-throated diver nest survival. Here I analyse red-throated diver nest survival information from three breeding seasons to; 1) obtain daily nest survival rates

(DSR) and the timing of breeding failure using nest temperature loggers; 2) evaluate stage-specific nest survival estimates and compare them with stage specific survival estimates from previous studies (Bundy 1976; Gomersall 1986; Dickson 1993; Eberl & Picman 1993); and 3) test the effects of nest age, breeding stage and year on nest survival. To do this, I make use of particular characteristics of red-throated diver breeding ecology; the results of previous red-throated diver research; and theories of optimal parental investment to develop a set of biologically relevant hypotheses relating to nest survival, which I use in an information-theoretic approach (Burnham & Anderson 2002) to inform the building of a set of candidate models which are then tested using the nest survival model in program MARK (White & Burnham 1999) . Specifically, I predict that:

1. Nest survival varies between study years because of the effects of known fluctuations in fish prey populations (Wright & Bailey 1996), annual variation in climatic conditions or predator pressures at key times in the breeding cycle.

2. Nest survival increases with nest age as a consequence of increased parental investment and/or because the sample of attempts were likely to include an increasing proportion of high quality birds.

3. Nest survival rate at the egg stage is different from the chick stage because of changes in predation risk as a consequence of either the negative effects of decreased vigilance by adults brought about by the mobility of chicks or positive effects resulting from predator avoidance by chicks.

3.3 Methods

I monitored red-throated diver nest survival in three breeding seasons (2006-8) at a total of 123 lakes on Mainland Shetland, Scotland. Ninety-three lakes were in four core study areas which were searched systematically to locate all breeding attempts. The remaining 30 were discrete water bodies outside core areas that were either known from historical information or found by chance (see section 1.3 '*Study sample*' for details of the characteristics of study lakes).

3.3.1 Breeding lake searches and confirming breeding

In the four core study areas all water bodies marked on 1:25,000 OS maps were searched for breeding pairs. In addition all land within the study areas was searched for the presence of small ponds not marked on OS maps, either by scanning with binoculars from vantage points or by adopting a time-per-unit-area search methodology (following Brown & Shepherd 1993). All shoreline was scanned with x10 binoculars and the entire perimeter of lake shorelines walked to locate active and non-active nests. I revisited lakes where pairs were present but where shoreline searches found no nest until I proved breeding or established that the site was vacant. A proven breeding attempt was one where eggs were seen in a nest or chicks were seen at a breeding lake which also contained a nest with hatched eggshell fragments within the nest material. An adult resting on the shoreline of a potential breeding lake is indistinguishable from an incubating bird (S.Hulka pers.obs.), so this alone did not qualify as proof of breeding. I verified the vacancy of sites by making a visit to all sites after the end of the incubation stage in late July to search for nests and hatched or predated eggshell remains. At all nests where intact eggs were not present I searched a radius of 10m around the nest to locate any predated eggshell remains.

Black-throated divers (*Gavia arctica)* construct ‘false nests’ that are not used for breeding (Cramp & Simmons 1977) and observations from this study suggest that this is also part of the breeding ecology of red-throated divers. It was not possible to differentiate these empty nests from those where eggs were laid and removed by a predator. Empty nests could not be included in the MARK nest survival analysis (see section 3.3.4 ‘*Preparing survival data for Program MARK’* below), however, excluding these nests inflates the survival estimate if they represent failed breeding attempts. I therefore recorded all empty nests to assess the extent of this bias.

No breeding lake contained more than one breeding attempt at any one time but second attempts were proven at a number of lakes after the first had failed. Although some experimental evidence suggests that failed pairs lay replacement clutches on the same lake (Schamel & Tracy 1985) I was not able to confirm or refute this, thus second and third attempts in this study have a spatial and temporal, but not necessarily a biological relationship to first attempts.

3.3.2 Recording nest fate

The nest survival model in MARK requires that nest fate can be correctly determined. Due to remoteness of red-throated diver breeding sites and their vulnerability to disturbance I only made two mandatory visits to breeding sites after a breeding attempt had been proven to determine the timing of failure or success; one around the predicted time of hatching and one to coincide with any surviving chicks reaching four weeks (see below). To help determine nest fate I made use of eggshell evidence in and around the nest. I assumed that nests with small fragments of eggshell (longest axis <10mm) present amongst nest material were the result of an egg or both eggs hatching. Nests with intact eggs recorded on one visit but on a subsequent visit without small eggshell fragments in the nest or with large eggshell fragments either crushed or punctured within a *ca.* 10m radius of the nest were recorded as predated. Out of 52 breeding attempts where at least one chick was seen, all but one had small eggshell fragments in the upper layer of nest material. Conversely, none of 14 nests where egg-laying was confirmed, but that were empty before the expected hatching date, had small eggshell fragments in the nest. In addition, none of 16 proven breeding attempts where large eggshell remains were found, and presumably were predated, had any evidence of surviving chicks. Thus, I concluded that a nest with hatched eggshell remains was a breeding attempt that had reached the chick rearing stage, and a nest where eggs ‘disappeared’ with no evidence of hatched eggshell remains in the nest material or predated eggshell remains on top of or within 10m of a nest, had failed during the egg stage. A potential difficulty when using eggshell fragments in nest material as evidence of hatching is that red-throated divers may use the same nest from year to year and as a consequence hatched eggshell fragments can survive from previous years (Alvo & Prior 1986). To minimize the chance of mistakenly using the presence of eggshells from previous years to determine the stage of failure I only categorised a nest as having hatched eggshell remains if it was found in the uppermost layer of the nest material and if there was no bleaching of the eggshell colour (Alvo & Prior 1986).

Weidinger (2007) examined the biases inherent in the different handling of uncertain nest fate data and proposed that in order to minimise bias in categorising nest fate, nest survival observations should be terminated at a point either before or at the earliest point at which the oldest fledgling can leave the nest. On Shetland, red-throated divers typically nest on discrete lakes which confine chicks until they are between six and eight weeks old when they are first able to fly either to an adjacent lake or the sea. Chicks grow to full size by four weeks and after that chick mortality is uncommon (Bundy 1976). To determine fledging success therefore, I timed a visit to all breeding sites to coincide with chicks reaching four weeks and terminated nest survival observations at this time. This allowed me to obtain survival information that was likely to be similar to true fledging success and by visiting breeding lakes before the chicks were able to fly ensured that the presence or absence of chicks denoted success or failure rather than departure from the breeding site and thus minimising nest fate uncertainty. Occasionally chicks move overland from very small nesting lakes to an adjacent larger water body (Bergman & Derksen 1977) or the sea (Fowler & Hicks 1986). I therefore checked all adjacent lakes up to the maximum documented distance moved by chicks of *ca* 400m to ensure that they were not present. Chicks from eight attempts at eight nest lakes moved to larger adjacent lakes during the course of the study.

3.3.3 Timing of breeding attempts

Timing of breeding estimates were required to; determine nest exposure time; calculate daily survival rates (see section 3.3.4 '*Preparing survival data for Program MARK*' below); and construct nest survival models that included nest age as a covariate using the nest survival model in MARK (see section 3.3.5 '*Statistical analysis*' below). To achieve this at as many breeding attempts as possible I made additional visits to breeding attempts to observe clutch increase or hatching. The average time interval between laying and hatching of first and second eggs for red-throated diver has been recorded as 2.3 days (SE = 0.3, N = 4) and 1.6 days (SE = 0.3, N = 7), respectively (Dickson 1993). Where I observed clutch increase from 1 to a complete clutch of 2 eggs, I defined laying date as the date that the first egg was observed. For full clutches where I observed the first egg hatching, I defined hatching date as one day after the visit date. For part-hatched full clutches and newly hatched single chick broods I defined the hatching date the same as the visit date. Although brooding at the nest may continue beyond a week, chicks are able to leave the nest within 24 hours of hatching (Cramp & Simmons 1977) and therefore chicks that make no attempt to leave the nest when the brooding adult is disturbed are likely to have recently hatched. In these cases I defined hatching date as one day before the nest visit. In addition to making supplementary observations at nest sites, I floated eggs (Westerkov 1950), recorded nest temperature during incubation using iButton® thermal data loggers (Model: DS 1922 L-F5 Thermochron, Maxim/Dallas Semiconductor Corp., Sunnyvale, CA) installed in the base of nests and recorded chick size by photographing chicks alongside adults. Using data from each of these techniques, I developed and validated linear regression models to estimate timing of breeding to *ca.* 4 days of the observed hatching date (see Chapter 2 for full details of timing of breeding model construction and validation). I back calculated from hatching date by a standardised red-throated diver incubation period of 27 days (Bundy 1976; Cramp & Simmons 1977) to obtain a laying date.

3.3.4 Preparing survival data for Program MARK

I used the nest survival model in 'program MARK' (White & Burnham 1999) to calculate the daily survival rate of nests in the sample and examine the effects of nest age and year for the sample of red-throated diver breeding attempts with known timing of breeding. MARK requires a minimum of five pieces of information about each nest to create an ‘encounter history’ which is used to calculate nest survival. These are 1) the date when a nest was discovered, 2) the date when the nest was last seen alive, 3) the date when the nest was last checked, 4) the fate of the nest (binary: successful = 0 or failed = 1) and 5) the number of nests that have the same sequence of information (Dinsmore *et al.* 2002). The date information in 1-3 is coded as a standardised number of days from the discovery of the first proven nest in the study. The earliest proven breeding attempt was 15 May. I defined this as day 1 of the study and for all other encounter occasions calculated the number of elapsed days from this date. The latest encounter occasion was 22 August (day 99). The 99 day period delineated by these two dates provided the ‘total number of encounter occasions’ required as summary input information in MARK. Table 3.1 gives the criteria that I used to determine the three pieces of date information used to describe survival for each nest. I excluded nests where the only observation was on the day of hatching or where the only observation was on the potential first fledging visit when chicks were four weeks or greater (*N* = 4). These nests were excluded because they were only under observation for one day and therefore provided no information with which to estimate survival (Dinsmore *et al*. 2002). Empty nests where no breeding was proven (*N* = 40 in the overall sample) were also excluded because it was not possible to determine a laying date or survival duration for these nests.

I coded the nest encounter information for each nest in two ways corresponding to egg stage and chick stage survival. Nests found during incubation and surviving beyond hatching were included in both groups. For example, a nest found with eggs on day 10; hatched on day 20; last seen active on day 25 and last visited on day 30 had an egg stage encounter history of '10 20 20 0 1'; and a chick stage encounter history of '20 25 30 1 1'. Nest fate was determined according to the outcome of the breeding stage and thus a nest that survived to hatching but failed during the chick rearing had different nest fate in each stage. Nests that failed during incubation or were only proven when chicks had already hatched, only occurred in egg or chick stage groups respectively. I divided each of the egg and chick stage encounter histories into three, corresponding to the study year, to obtain six groups with stage and year effects (following Dinsmore & Dinsmore 2007).

3.3.5 Statistical Analysis

First, I calculated the daily survival rate for first and second attempts using the intercept only, thus fitting a model that assumed constant survival throughout the study period. This model is comparable to the Mayfield estimator and allowed me to compare survival from this study with Gomersall’s (1986) earlier estimates. I derived cumulative survival rates for egg and chick stages and overall nest survival (assuming 27 days for incubation and 28 days for chick rearing). To test for differences in daily survival rate between first and second attempts I used an independent t-test with Welch’s correction to allow for unequal variance between group means. To test for differences in daily survival rate between year and breeding stage I used 2-way ANOVA and Bonferroni post hoc tests to identify the source of any significant differences. These analyses were carried out using SPSS (SPSS Inc. version 15). Tests were two-tailed with the significance level set at $P = 0.05$. Means with ± 1 standard error or medians with a range are reported.

I evaluated six candidate models to test the hypotheses relating to the effects of year, nest age and breeding stage on nest survival. In addition to an intercept only model where survival was held constant (model 4), I tested models that included linear and quadratic effects of nest age (models 1 and 2, respectively), and categorical effects of breeding stage (model 3) and year (model 6). I also tested additive effect of breeding stage and year (model 5). I included a quadratic effect of nest age because previous studies found relatively high mortality during early incubation and early chick rearing suggesting that nest survival may not follow a linear trend. To construct models that included nest age, I followed the procedure in (Rotella 2005) allowing daily survival rate to follow a trend with respect to nest age. I used the default sine and logit link functions for constant survival and covariate models, respectively (White & Burnham 1999). I used Akaike's Information Criterion value corrected for small sample sizes (AIC_c) to rank competing models with the model best supporting the data identified as that with the lowest (AIC_c) value. I used the associated Akaike weight (W_i) to quantify the degree of support between competing models and assumed that there was support for a difference between two models if the ΔAIC_c values differed by greater than 2.0. To examine the variation in daily survival rate through the breeding cycle for specific models, I used parameter estimates and back transformed these from the logit scale to obtain real parameter estimates (Dinsmore *et al.* 2002; Rotella 2005). The nest survival model in MARK assumes that nest fates are independent. I therefore restricted model building analysis to first breeding attempts because second breeding attempts occurred on the same lakes and may have involved one or both of the adults from the first attempt. Separate analysis of second breeding attempts was not feasible due to the small sample size of second attempts with timing of breeding information ($N = 16$).

At breeding attempts where laying date was known and temperature loggers installed, I also determined the duration of clutch survival before failure and timing of failure for each nest by identifying the time that plotted nest temperatures converged with simultaneously recorded ambient temperatures. I corroborated this with a predicted estimate obtained by fitting a quantitatively determined convergence date that estimated nest abandonment after hatching to a regression model (see Chapter 2, section 2.3.2, *Nest temperature models*-convergence of nest and ambient temperature model). On average this model over-estimated the plotted time of convergence by 0.7 ± 0.15 days (*N* = 12). I rounded each failure time to the nearest 4-hour block that I assumed; based on previous observations, reflected differing levels of diver activity at breeding lakes (S.Hulka pers.obs). These were: 23:00 – 02:59 (hours of darkness), low activity associated with sleeping or inactivity with both adults usually present; 03:00 – 06:59 (dawn), moderate activity associated with alternate foraging sorties by adults; 07:00 – 10:59 (morning), high activity associated with foraging sorties, territorial flights by one or both parents and territorial encounters on the breeding lake; 11:00 - 14:59 (mid-day), low activity associated with continuous incubation, with the off-duty adult frequently absent; 15:00 - 18:59 (afternoon), low to moderate activity associated with continuous incubation and foraging sorties by adults; 19:00 – 22:59 (evening), moderate activity levels associated with alternate foraging sorties by adults.

3.4 Results

One hundred and three first attempts at 66 different lakes and 16 second breeding attempts at 15 different lakes had timing of breeding dates and survival information suitable for the MARK analysis. This represented 42% and 50% of the total number of monitored first and second breeding attempts, respectively. For breeding attempts where timing of breeding estimates were obtained from observation of laying or hatching (*N* = 4, *N* = 16, respectively) or where a flotation estimate was available (*N* = 68) I used these. Of the 31 remaining attempts 30 had a single estimate derived from either chick size (*N* = 21) or peak nest temperature models (*N* = 9) and I used these estimates. The remaining attempt had chick size and peak nest temperature estimates that were the same so I used this estimate.

The average DSR for first attempts using the model assuming constant survival was 0.988 ± 0.002 (N = 103) giving a cumulative probability of survival over a 55 days breeding cycle (27 day incubation + 28 day chick rearing) of 0.51 ± 0.011, suggesting that approximately half of the first breeding attempts succeeded in raising at least one chick to at least 4 weeks. DSR estimates of stage-specific survival were higher for the chick stage than for the egg stage in all three study years (Table 3.2), however the effect of breeding stage on year was not significant (two-way ANOVA: $F_{1,612} = 3.25$, $P = 0.07$) although Bonferroni post hoc tests did reveal that in 2008 DSR was significantly higher at the chick stage (P <0.05) than in the other two years. Neither the effect of year on breeding stage nor the interaction of year and breeding stage were significant (two-way ANOVA: $F_{2,612} = 1.12$, $P = 0.33$; $F_{2,612} = 1.52$, $P = 0.22$ respectively). The average DSR for second breeding attempts was 0.961 ± 0.01 (N = 16) corresponding to a cumulative survival probability of 0.11 ±0.13. Hence, DSR rates were significantly higher for first compared with second breeding attempts ($t_{16} = 2.65$, $P = 0.02$).

Of the six models that I used to test the *a priori* hypotheses relating to patterns of survival through the breeding cycle, the model with an effect of nest age (model 1) was best supported by the data. Adding a quadratic term to the nest age (model 2) resulted in a model which, although still supported, with a ΔAIC_c value of less than 2, had not increased support for the individual effect of nest age. Hence, I concluded that model 1 was relatively better supported than model 2. (Table 3.3). When model 2 was not included in the candidate set the individual nest age model explained 75% of the variation in the data. The intercept model that assumed that survival was constant (model 4) was unsupported as were models with individual or additive effects of year and breeding stage (models 3, 5 and 6). Fitting beta estimates from the best model to each day of the 55 days of the breeding cycle suggested that survival increased with nest age (Figure 3.1).

For 12 breeding attempts that failed during the egg stage and where temperature loggers were installed and laying date was known, average clutch survival was 9.2 ± 1.44 days. There was no significant difference in clutch survival between first (median = 9 5 d, range 2 -14, N = 8) and second breeding attempts (median = 10.5 d, range 3 -16, *N* = 4; U = 12.0, *P* = 0.53). Failure occurred most frequently in the afternoon period between 15:00 and 18:59 (4 nests) and during hours of darkness between 23:00 and 02:59 (3 nests). There were no failures in the morning between 07:00 and 10:59.

Table 3.1.Observational and circumstantial evidence used when determining the three pieces of date information required to run survival analyses in Program MARK. The date information in 1-3 is coded as a standardised number of days from the discovery of the first proven attempt in the study. The 'Termination date' is the terminal dates allowed for each breeding outcome in each of the analyses.

	Nest fate	**1) active nest found**	**2) date last seen active**	**3) date last checked (outcome determined)**	**Termination date**
Egg stage	**Failed**	Egg/s or incubating bird seen	Egg/s or incubating bird seen	Empty nest with no hatched eggshell or nest with predated eggshell in vicinity of nest	Date last checked or hatching date determined from egg flotation
	Successful	Egg/s or incubating bird seen	Hatching observed or hatched eggshell fragments in nest	Hatching observed or hatched eggshell fragments in nest	Observed hatching date or hatching date determined from predictive models
Chick stage	**Failed**	Chick(s) seen or hatched eggshell in nest	Chick(s) seen or hatched eggshell in nest	Chick(s) absent from, or predated chicks found at breeding lake	Date last checked or, potential first fledging date (4 weeks after hatching determined from predictive models)
	Successful	Chick(s) seen or hatched eggshell in nest	Chick(s) seen	Chick(s) seen	Potential first fledging date (4 weeks after hatching determined from predictive models)

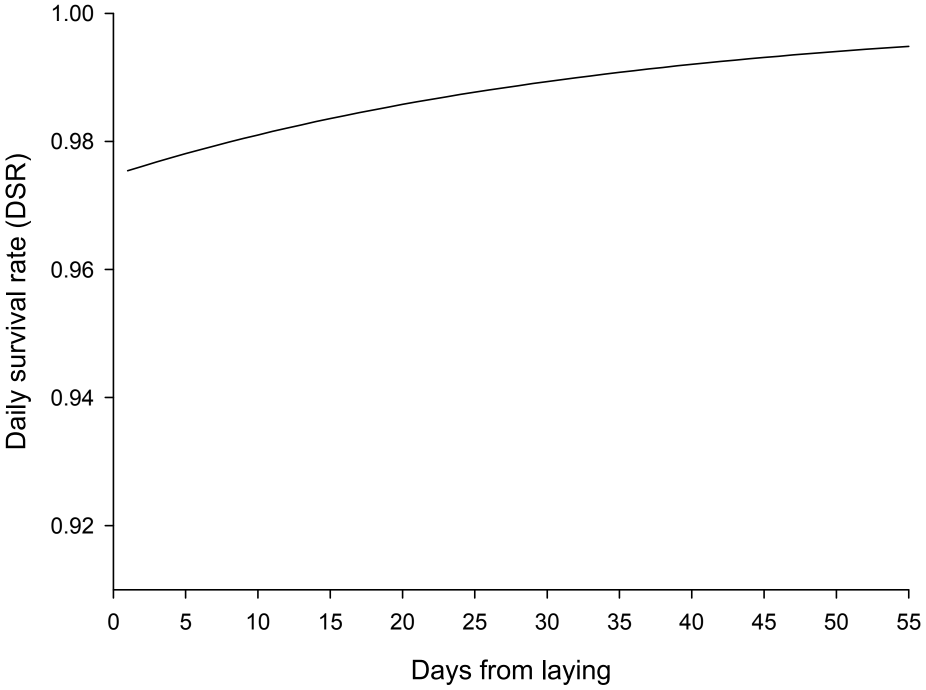
Table 3.2 Egg stage, chick stage and overall daily survival rates (DSR) for red-throated diver first attempts, Mainland Shetland, Scotland, 2006-2008. Mean DSR and ±1SE are parameter estimates from the intercept model (model 4, Table 3.3) which assumes constant survival within and between years. Numbers in parentheses give the cumulative survival figures for a 27 day egg stage; 28 day chick stage and an overall breeding cycle of 55 days.

	Egg stage		Chick stage		Overall nest survival	
	DSR	±1SE	DSR	±1SE	DSR	±1SE
2006	0.988 (0.71)	0.005	0.989 (0.74)	0.004	0.988 (0.53)	0.003
2007	0.987 (0.71)	0.004	0.991 (0.79)	0.003	0.989 (0.55)	0.003
2008	0.973 (0.47)	0.009	0.991 (0.78)	0.004	0.983 (0.40)	0.005
All years	0.984 (0.65)	0.003	0.991 (0.77)	0.002	0.988 (0.51)	0.002

Table 3.3 Model selection results for red-throated diver nest survival through the breeding cycle, Mainland Shetland, Scotland, 2006-8. AIC$_c$ = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of ÄAIC$_{c;}$ values. The intercept only model assumes that survival is constant. Covariates included in the model set were; study year; nest age and breeding stage (assuming an egg stage of 27 days and a chick stage of 28 days).

Model No.	Model name	Deviance	Parameters	AIC$_c$	Δ AIC$_c$	AIC$_c$ Weight (w$_i$)
1	Nest age	230.78	2	234.78	0.00	0.51
2	Nest age + nest age^2	229.70	3	235.71	0.93	0.32
3	Breeding stage	234.28	2	238.29	3.50	0.09
4	Intercept	237.12	1	239.13	4.34	0.06
5	Year + breeding stage	235.67	3	241.68	6.90	0.02
6	Year	230.96	6	242.98	8.20	0.01

Figure 3.1 Daily survival rate (DSR) for red-throated diver, estimated from the best supported model with an effect of nest age (egg-stage = 27 days, chick stage = 28 days.)



3.5 Discussion

Daily survival rate (DSR) was not constant through the breeding cycle and the intercept model, where survival was held constant, corresponding to the commonly used Mayfield estimator (Mayfield 1975) received little support. This corroborates the findings of an increasing number of studies (e.g. Dinsmore *et al.* 2002; Grant *et al.* 2005) that the Mayfield estimator is often an unrealistic and relatively uninformative nest survival model as it does not reveal time-specific patterns that may provide important clues to the underlying ecological and population processes affecting variation in nest survival.

Differences in DSR between study years were similar, suggesting some underlying stability in nest survival risk through the breeding cycle. The sample of nest lakes were the same for all study years and in many cases actual nest sites were in the same location for more than one year. This constancy of breeding location within the sample may have been reflected in similar levels of predation risk and this may in part explain the stability in survival levels between years. Between-year similarities may also suggest that external factors such as environmental conditions, food and predator abundance had a net constant effect because positive effects compensated for negative ones or no had no effect on stage-specific survival. The reuse of the same breeding lakes and in some cases nests between years may result in data points that are not strictly independent because the same individuals may have been involved. In view of this, marginally significant results should be regarded with some caution.

Daily survival rate was significantly higher for first compared with second breeding attempts. Laying dates for second attempts were widely scattered through the breeding season (median 20 June, range 21 May - 25 July) and therefore environmental conditions and food availability were likely to be similar to those of first attempts, suggesting that these factors were not important in explaining the high failure rate of second attempts. The low survival rate of second breeding attempts could be explained if these pairs were low quality, late breeders taking over a failed site, as this section of the population are more likely to fail and breed later (Lack 1968; Perrins 1970). Alternatively, nest survival rate for renesting first attempts may be lower because resources expended during the first attempt reduce the effectiveness of protecting a second attempt. Additionally, experimental field tests (Enquist 1983) found that Arctic skuas employed landscape features to memorise the location of red-throated diver nests, revisiting them to check if they were re-occupied. This increased awareness and memorising of breeding sites by a potential predator is also likely to increase the predation risk for second attempts at breeding sites where the initial attempt was predated earlier in the breeding season and could explain the relatively high failure rate of second attempts.

The number of nests failing at the egg stage was significantly higher than at chick stage and although DSR estimates reflected this when averaged for each stage the differences were not significant. This result may have occurred because variation in nest survival was not stage specific and instead reflected a gradual change with nest age.

Compared with this study, stage specific survival estimates reported by Gomersall (1986) from 168 breeding attempts on Shetland, were lower for both the egg stage (0.5, ±0.06) and the chick stage (0.6, ±0.07), but not significantly so. Moreover, these differences may have occurred because second attempts with lower survival rates were included in Gomersall's sample. Stage specific estimates did corroborate the findings of earlier studies that egg stage survival is lower than chick stage survival in red-throated divers.

In each study year a recently constructed nest with no eggs or eggshell fragments was the only evidence of breeding activity at approximately 15% of lakes. The lack of survival information about these nests resulted in them being excluded from the MARK analysis. It is likely that at least some of these nests were failed breeding attempts that survived briefly, suggesting that the low egg stage survival rate was an overestimate and further emphasises the vulnerability of the red-throated diver incubation period. Future studies should attempt to quantify the proportion of empty nests that are failed nests and the extent to which this varies between years to obtain a weighting that can be applied to improve accuracy of DSR estimates. Low cost temperature data loggers such as those used in this study, installed in the base of empty nests and set to record nest temperature at regular intervals would reveal whether nests were occupied without the need for multiple field visits. Furthermore, these temperature records would provide survival information such as time of laying and time of failure or hatching. Fitting these data to nest temperature models developed in Chapter 2 would allow timing of breeding to be estimated for these nests, thus providing all the information required for inclusion in the MARK nest survival model.

Constraints on the number of breeding lake visits that were possible and/or desirable during the season resulted in relatively wide confidence intervals when DSR rate were translated into cumulative survival rates for the egg and chick stages. To improve future nest survival estimates for red-throated divers and other difficult to monitor or vulnerable species, nest-installed temperature loggers have the potential to provide more accurate data for egg stage survival analysis with minimal disturbance to breeding birds. At the chick stage, red-throated diver chicks are typically confined to a small breeding lake and this offers the possibility of effectively monitoring survival using relatively cheap digital ‘game’ camera units, trained on the breeding lake and set to record periodically and/or to be triggered by movement.

Red-throated diver nest survival was best explained by a model with a linear effect of nest age that suggested DSR increased with nest age. Red-throated diver egg stage activity at the breeding lake is minimal; incubation is largely continuous, nest changeovers infrequent and the off-duty parent is usually absent (Natural Research unpubl. data). As a consequence, the cues to potential visually hunting predators are minimised (Martin *et al*. 2000). By contrast during the chick rearing stage parents and chicks are increasingly present on the open water and adults make frequent conspicuous provisioning flights to and from the breeding lake (Reimchen & Douglas 1984), which can give cues to predators or result in increased separation between the attendant adult and chick(s), increasing their vulnerability to predator attacks. If variation in nest survival were primarily explained by the exposure of eggs and chicks to predators then these behaviours should result in a strong support for a model that included the effect of breeding stage and a decreasing trend in nest survival as the breeding cycle progresses. I found no support for an effect of breeding stage and the best model indicated that DSR increased incrementally as the breeding cycle progressed suggesting that variation in DSR is to some degree independent of the constraints imposed on parental protection by stage specific breeding ecology. Increasing parental effort with nest age better explains the pattern of increasing nest survival rate as the breeding cycle progresses. However, although DSR shows a clear increase throughout the egg stage the increase appears to slow during the chick stage. If increasing parental effort was the main factor influencing the survival pattern described by the nest age model it seems likely that survival would continue to improve throughout the breeding cycle. Furthermore, some of the most successful breeding pairs consistently reacted to the earliest indication of a predator by leaving the nest and flying off the breeding lake regardless of the stage of incubation. Alternatively, this pattern may be due to selective mortality of nests whereby poorer quality birds fail early during the egg stage leaving a higher proportion of higher quality individuals that are more likely to succeed as the breeding cycle progresses. I evaluate the effect of individual quality on nest survival more fully in Chapter 4. Another possibility is that the quality of nest site is a key factor in determining nest survival in red-throated diver. This may occur if nest site characteristics are related to predation risk or the effects of environmental conditions, leading to more vulnerable sites failing early in the breeding cycle. I explore the effect of nest site characteristics on red-throated diver nest survival in Chapter 5.

4 The effects of date and individual quality on red-throated diver nest survival

4.1 Abstract

Timing of breeding can have important fitness consequences for birds because the considerable demands of reproduction must be matched by food resources available for both adults and young. Furthermore, it is generally recognised that the earliest birds to breed are often the most successful and that breeding performance declines with date. This may be because poorer quality birds breed later and are therefore more likely to fail or because key environmental factors decline as the breeding season progresses. Here I explore whether nest survival of red-throated divers varies through the season, what shape this relationship has, and whether some attributes of individual quality further contribute to it. The highest survival rates were early in the season and survival rate did decline with date. However birds with larger egg volumes per clutch, presumably the higher quality birds, showed a lower rate of decline compared with birds with smaller egg volumes.

4.2 Introduction

Timing of breeding is an important determinant of fitness in birds (Perrins 1970) because breeding successfully requires that the energy demands of reproduction coincide with peak food availability (Lack 1968). In seasonally breeding birds the effects of human induced climate change has led to increases in sea surface temperatures which have in turn resulted in the altered timing and abundance of key prey items (Shultz *et al.* 2009). At high latitudes this problem may be particularly acute because the time window when food availability and other conditions for breeding are suitable is short and therefore the possibility of adjusting to shifts in timing is limited. Overall the onset of breeding is hormonally controlled and the exact timing may be modulated by non-photoperiodic environmental cues (Dawson 2007). Local conditions on the breeding grounds should provide the most reliable cues but migratory species or species that disperse widely during the non-breeding season may have to rely on larger scale cues which may be less reliable (Frederiksen *et al.* 2004; Visser & Both 2005). The reliability of these cues may be reduced further because the effects of climate change may be different in non breeding areas compared with breeding areas.

It is generally recognised that birds that breed early generally produce most recruits into the population (e.g. Perrins 1965; Hochachka 1990) and this should therefore lead to directional selection for early breeding. However, because breeding is determined by the females having sufficient energetic resources to produce eggs, this temporal pattern in breeding performance can be different depending on the timing of peak food availability. For example, van Noordwijk (1980) found that in some years late broods can do better than early ones when food availability is highest later in the year. There is also some evidence that the very earliest breeders are less successful (Perrins & McCleery 1989). Other factors may also affect this general pattern. For example breeding birds have been shown to track predation risk (Fontaine & Martin 2006) and thus peak nest initiation may correspond to a peak in daily survival rate, provided nest predation is not density dependent, because the majority of nests will be initiated when predation risk is lowest (Kroll & Haufler 2009).

Seasonal change in breeding success is not well understood because timing of breeding is often confounded with aspects of quality. In this context, quality may be the phenotypic quality or body condition of breeding individuals or the quality of their breeding environment, in particular the quality of breeding sites, territories, foraging areas or food (Verhulst & Nilsson 2008). For example, early breeding birds may be; older/more experienced (e.g. de Forest & Gaston 1996), occupy food rich breeding territories (Daan *et al.* 1990), or in better nutritional condition (Lack 1966; Davis & Lundburg 1985; Arcese & Smith 1988). However, these high quality traits are likely to be correlated with high breeding success independent of laying date (Nilsson & Svensson 1993). Two hypotheses are used to explain these relationships. The 'date hypothesis' states that the seasonal pattern in reproductive performance relates to factors associated with the date of laying, such as environmental conditions which will affect all individuals in the same way (Verhulst & Nilsson 2008). The effect of date may be absolute; for example when breeding is constrained by a physiological process such as post-breeding moult (Svensson & Nilsson 1997) or relative; for example, when breeding is related to the abundance of conspecifics breeding in the same area, in which case the benefits may relate to increased vigilance or dilution of predation pressure (Hatchwell 1991); or is related to a seasonal environmental change such as peaks in prey abundance (Perrins 1965). The 'quality hypothesis' assumes that these seasonal patterns reflect differences in quality, irrespective of timing of breeding (Arnold *et al.* 2004; Verhulst & Nilsson 2008). Experimental studies are necessary to distinguish between these two possibilities (reviewed in Verhulst & Nilsson 2008). Some suggest that seasonal change in breeding success is entirely due to quality (de Forest & Gaston 1996; Hipfner 1997), due to date (Moreno *et al.* 1997) or both the date and quality hypotheses are important (Verhulst *et al.* 1995; Brinkhof *et al.* 1997).

The red-throated diver predominantly breeds in arctic and sub-arctic tundra, nesting in open locations along the shoreline of small inland lakes where chicks are typically confined until they are able to fly off when they are between six and eight weeks (Bundy 1976; Cramp & Simmons 1977). Throughout much of their breeding range the length of time available for breeding is limited by the date when breeding lakes thaw in spring and refreeze in late summer (see Dickson 1993). This exerts a relative date constraint on the availability of the breeding lake and thus a selective pressure on the timing of breeding that should favour early breeding, as to breed later would risk failure due to offspring being unable to fly before refreezing occurred. However, it may be only the higher quality individuals that have adequate nutritional resources for egg formation on arrival on the breeding grounds that are able to breed early. Another possibility is that nest survival and breeding success are related to a peak in food availability. Rindorf *et al.* (2000) found that peak availability of the lesser sandeel (*Ammodytes marinus*) in the North Sea was in June and this corresponded with increased seabird breeding success. Compared with other fish prey taken by red-throated divers, sandeels are of high calorific value (Hislop *et al.* 1991) and therefore peak availability of sandeels may reflect a peak in nest survival. On Shetland, the red-throated diver breeding season starts in May, so birds breeding early in the season are likely to raise chicks at a time of peak sandeel abundance whereas those breeding late will miss this peak. The principal proximate cause of breeding failure in red-throated divers is avian or mammalian predation (Bundy 1976; Bergman & Derksen 1977; Gomersall 1986;

Dickson 1993; Eberl & Picman 1993; Dahlén & Eriksson 2002). If females are able to assess predation risk (Fontaine & Martin 2006) then peak nest initiation should correspond to a peak in daily survival rate, provided nest predation is not density dependent, because the majority of nests will be initiated when predation risk is lowest (Kroll & Haufler 2009).

Here I assess whether the breeding performance of red-throated divers varies through the breeding season, what shape this relationship has (linear or peaked curve), and whether some attributes of individual quality further contribute to it. I used egg volume per clutch and clutch size as two indices of individual quality. Egg volume and clutch size have been demonstrated to reflect a number of ‘quality’ attributes in birds. For example females in better condition may produce larger clutches (Nager 2006) and older females and/or females in better condition produce larger eggs (Christians 2002). Egg volume may also be related to chick quality (Slattery & Alisauskas 1995; Nager *et al.* 2000). For example, females laying larger eggs may have hatchlings that are larger (Ricklefs *et al.* 1978; Dawson & Clark 1996); have greater nutritional resources (Slattery & Alisauskas 1995); and that are better able to survive the initial stages of the chick rearing period (Ankney 1980; Slattery & Alisauskas 1995). Furthermore, egg size may reflect the quality of the male parent as well as the female because the degree of paternal investment in the pre-laying stage of a breeding attempt may affect the resources that the female is able to invest in egg production (Nisbet 1973; Coulson 1976) and females tend to choose mates of similar age and hence similar quality (Nisbet *et al.* 1984).

I use a model building approach (Burnham & Anderson 2002) implemented using the nest survival model in program MARK (White & Burnham 1999) to test the relative importance of these effects. I draw on general research that examines the influence of date and the quality of the breeding pair on reproductive success and more specific research examining red-throated diver breeding performance to develop a set of relevant hypotheses. I use these to inform the building of a set of candidate models designed to examine the influence of these factors on red-throated diver nest survival.

Specifically, I predict:

1. Daily nest survival rates decrease with laying date due either to changes in food availability, changes in predation risk or the quality of breeding pairs.

2. Daily nest survival rate peaks at a particular point in the breeding season and that this relates to either a peak in availability of preferred prey or a period of minimal predation risk.

3. Average egg volume per clutch and clutch size are positively associated with daily survival rate because better quality females would lay more and larger eggs, be paired with males of similar quality, and as a result have better reproductive success than pairs in poorer condition.

4.3 Methods

I collected nest survival information, and measured egg size and clutch size during monitoring of 123 breeding lakes in three breeding seasons (2006-8) on Mainland Shetland, Scotland, as part of wider research on red-throated diver breeding biology. During the egg laying period, which including replacement clutches extends from early May to late July on Shetland (Bundy 1976; Gomersall 1986 Natural Research unpubl. data), I made 100% shoreline searches to confirm breeding and determine nest fate. During the main chick-rearing period between late June and mid August I made follow-up visits to determine nest fate for all breeding attempts (see Chapter 3 for a description of search methods and criteria for confirming breeding and determining nest fate). Where incubation was proven I made a licensed nest visit to; float eggs (Westerkov 1950); install iButton® temperature data loggers (Model: DS 1922 L-F5 Thermochron: Maxim/Dallas Semiconductor Corp., Sunnyvale, CA) in the base of nests; and take photographs of chicks alongside adults. Using data from each of these techniques, I developed and validated linear regression models to estimate timing of breeding to *ca.* 4 days of the observed hatching date (see Chapter 2 for full details of timing of breeding model construction and validation). I back calculated from hatching date by a standardised red-throated diver incubation period of 27 days (Bundy 1976; Cramp & Simmons 1977) to obtain a laying date. During a nest visit I also measured egg dimensions and recorded clutch size.

To measure eggs I first took a photograph of the undisturbed nest which I used as a reference to reposition eggs after measuring them. I removed eggs one at a time and took one measure of egg length and two measures of egg width at the widest point using digital callipers to the nearest 0.01 mm. I replaced the eggs to the same position in the nest using the reference photograph as a guide. I recorded clutch size as part of the nest visit. To calculate egg volume I used an egg volume coefficient of 0.51 reported by Stonehouse (1963) in Hoyt (1979) for 10 seabird species and used the equation: egg volume (cm^3) = $width^2 \times length \times$ egg volume coefficient (0.51) (Hoyt 1979). In the analysis I used average egg volume for two-egg clutches and volume of the individual egg for one-egg clutches. I assumed that clutches were incomplete if only one egg was present and attempted to revisit the breeding lake within a week to confirm clutch size. Few nests were visited frequently enough during egg laying to ensure that the recorded number of eggs was the true clutch size and not a partially predated clutch, however, previous fieldwork (2004-6) of approximately 100 breeding attempts in this study area did not confirm any partial clutch loss (Natural Research unpubl. data), and I therefore assumed that the recorded number of eggs reflected the true clutch size.

4.3.1 Statistical Analysis

First, I tested for differences in egg volume. I used one-way ANOVA to compare variance in egg volume within and between clutches. I used two-way ANOVA to test for differences in average egg volume between; study years, first and second attempts, and one and two egg clutches. I tested for differences in laying date between years using a one-way ANOVA. For first attempts only, I tested for a relationship between laying date and average egg volume per clutch using Pearson's correlation, and between laying date and clutch size using logistic regression. Statistical tests were carried out using SPSS (SPSS Inc. version 15). All tests were two-tailed with the significance level set at $P = 0.05$ and were checked for assumptions of normality. I checked for significant variance between sample groups using Levene's test and report the t-test statistics that reflect the results of this test. Means with ± 1 standard error of the mean are reported.

I used the nest survival model in program MARK (White & Burnham 1999) (see Chapter 3, section 3.3.4, *Preparing survival data for Program MARK,* for details of data preparation for nest survival modelling using MARK) to evaluate 11 candidate models based on the predictions I made relating to the effects of timing of breeding and egg size on nest survival. In addition to an intercept only model where survival was held constant throughout the study period, I fitted a model with an effect of laying date to examine whether survival rate decreased with date to test hypothesis (1). I added a quadratic effect to this model to examine whether there was evidence of a peak in nest survival to test hypothesis (2). To model the influence of individual quality as proposed in hypothesis (3), I tested individual covariates of average egg volume per clutch and clutch size. I also tested for an effect of year in relation to laying date, average egg volume per clutch and clutch size. After fitting models I tested if the best supported of these was improved by adding an effect of the second best supported model. A model with an effect of nest age best explained nest survival through the breeding cycle in Chapter 3, so I re-ran this model with this dataset to examine its influence compared with laying date and egg size. I used the 'power' function in MARK to obtain a quadratic effect of laying date (following Rotella 2005). I did not standardise covariates and used the default sine and logit link functions for constant survival and covariate models respectively (White & Burnham 1999).

I used Akaike's Information Criterion value corrected for small sample sizes (AIC_c) to rank competing models with the model best supporting the data identified as that with the lowest (AIC_c) value. I used the associated Akaike weight (W_i) to quantify the degree of support between competing models and assumed that there was considerable support for a difference between two models if the ΔAIC_c values differed by greater than 2.0. To examine the variation in DSR through the breeding cycle for specific models I used parameter estimates and back transformed these from the logit scale to obtain untransformed parameter estimates (Dinsmore *et al.* 2002; Rotella 2005). The nest survival model in MARK assumes that nest fates are independent. I therefore restricted model building analysis to first breeding attempts because second breeding attempts occurred on the same lakes and may have involved one or both of the adults from the first attempt. Separate analysis of second attempts was not feasible because the number of second attempts where egg size was recorded was small ($N = 14$).

4.4 Results

I measured egg size dimensions and recorded clutch size at 90 nests; 28 in 2006, 46 in 2007 and 16 in 2008. Table 4.1 gives the average egg volume of one-egg clutches and smaller and larger eggs in two-egg clutches for first and second attempts. The average egg volume per clutch for all nests was 77.88 ± 0.64 cm^3 ($N = 90$). The proportion of one to two-egg clutches was very similar between attempts with 75% of first and 71% of second attempts having 2-egg clutches ($\chi^2_1 = 0.08$, $P = 0.79$). The largest egg in the sample had a volume that was 59% greater than the smallest. This is similar to the average within-species egg size difference found in a review of 39 egg size studies (Christians 2002).

For two egg clutches eighty-six percent of the variation in egg volume was due to differences between rather than within clutches (one-way ANOVA, $F_{66,67} = 6.39$, $P < 0.001$). There was no significant difference in average egg volume for first and second attempts ($F_{1,75} = 0.02$,$P = 0.89$) or between years ($F_{2,76} = 0.29$, $P = 0.75$). However two egg clutches had significantly larger eggs than one egg clutches ($F_{1,78} = 8.80$, $P = 0.004$, Figure 4.1). There was a significant difference in laying dates between the three study years (one-way ANOVA, $F_{2,77} = 4.24$, $P = 0.02$). For first attempts, I found no correlation between average egg volume per clutch and laying date ($r = -0.18$, $P = 0.16$, $N = 67$), but there was a significant decrease in clutch size related to laying date ($\chi^2_1 = 6.32$, $P = 0.012$).

Daily nest survival rates from the intercept only model averaged for the 27 day egg-stage were lower for one-egg clutches (0.52 ± 0.10) compared with two-egg clutches (0.65 ± 0.05).

Sixty seven first attempts (14 with one-egg clutches and 53 two-egg clutches) also had reliable estimates of laying date and these were used to evaluate the effects of laying date and egg size on nest survival in MARK. Of the 11 models that I used to test the *a priori* hypotheses relating to the influence of date and quality on nest survival, the model combining the effects of laying date and average egg volume was the best supported (model 1 in Table 4.2, Figure 4.2). Models with individual effects of laying date (model 2, Figure 4.3) and average egg volume (model 3, Figure 4.4) were also supported. The individual and additive effects of these models explained 62% of the variation in the data. In addition to these, a model with an effect of nest age (model 4, Figure 4.5) was supported. The constant survival model (model 8) received no support. Models with additive effects of year and laydate or egg volume (models 5 and 7) or a quadratic effect of laydate (model 6) were not supported but performed slightly better than intercept only. Models with an individual effect of clutch size or additive effects of clutch size and year performed less well than the intercept model.

Table 4.1 Average egg volume of 1-egg clutches; smaller, larger and both eggs in 2-egg clutches for first and second red-throated diver breeding attempts, Mainland Shetland, Scotland, 2006-2008.

	First attempts		Second attempts	
Clutch size	*N*	Egg volume (cm^3)	*N*	Egg volume (cm^3)
1-egg	19	74 ± 1.2	4	75.1 ± 1.3
2-egg (smaller)	57	77.3 ± 0.8	10	77.1 ± 1.5
2-egg (larger)	57	81 ± 0.8	10	81 ± 1.5.
2-egg (average)	57	79.2 ± 0.8	10	79 ± 1.5

Table 4.2 Model selection results for the effects of date and individual quality on red-throated diver nest survival compared with the best supported model from the variation through the breeding cycle analysis (Chapter 3, nest age model), Mainland Shetland, Scotland, 2006-8. AIC_C = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of $\Delta AIC_{c;}$ values. The intercept model assumes survival is the constant.

Model No.	Model	Deviance	Parameters	AIC_c	Δ AIC_c	AIC_c Weight (w_i)
1	Laying date + egg volume	155.76	3	161.77	0.00	0.29
2	Laying date	158.90	2	162.90	1.13	0.17
3	Egg volume	158.96	2	162.96	1.19	0.16
4	Nest age	159.58	2	163.59	1.82	0.12
5	Year + laying date	156.16	4	164.19	2.42	0.09
6	Laying date + laying date^2	158.29	3	164.30	2.53	0.08
7	Year + egg volume	158.08	4	166.11	4.34	0.03
8	Intercept	164.46	1	166.46	4.69	0.03
9	Clutch size	163.52	2	167.53	5.76	0.02
10	Year	163.49	3	169.51	7.74	0.01
11	Year + clutch size	162.70	4	170.73	8.96	0.00

Figure 4.1 Frequency distribution showing the average egg volume of 1-egg clutches and smaller and larger eggs within 2-egg clutches for first and second red-throated diver breeding attempts combined, Mainland Shetland, Scotland, 2006-2008.

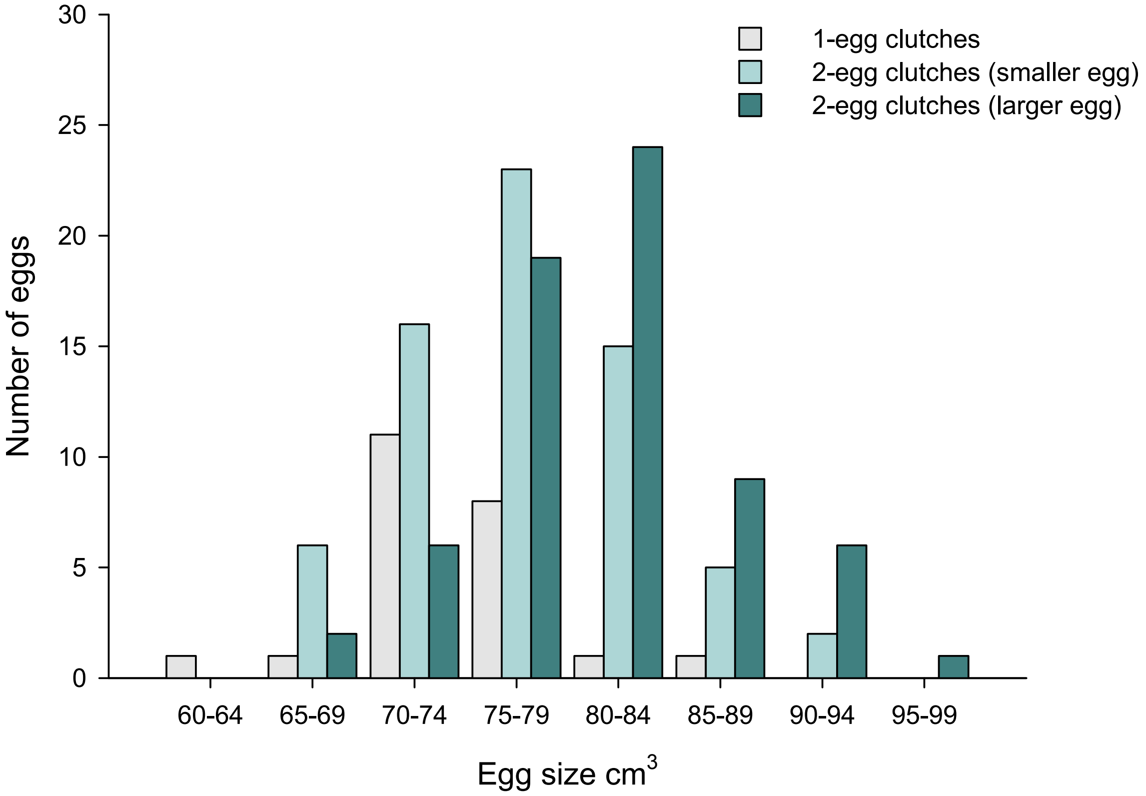


Figure 4.2 Daily survival rates (DSR) for red-throated diver estimated from best supported model that includes an additive effect of laying date and egg volume (model 1). Solid line represents DSR for the largest egg volume (94 cm^3), and dotted line, DSR for smallest egg volume (61 cm^3) in the sample. The grey bars show the number of nest initiations in 5 day blocks. The model uses egg and chick stage survival information.

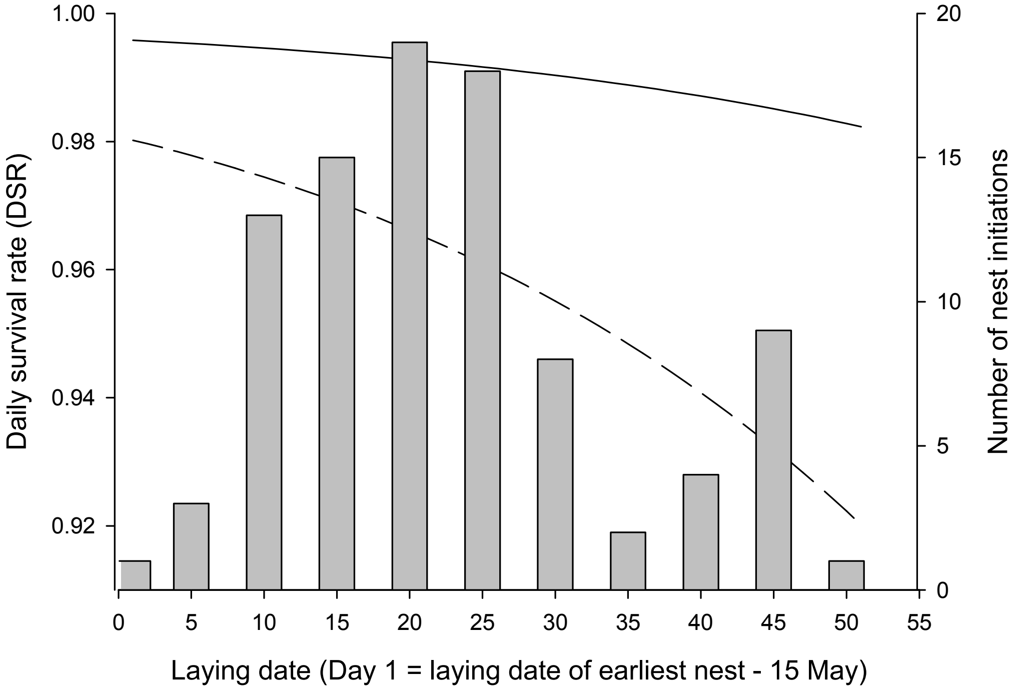


Figure 4.3 Daily survival rate (DSR) for red-throated diver estimated for the second best supported model with an individual effect of laying date (model 2) The model uses egg and chick stage survival information.

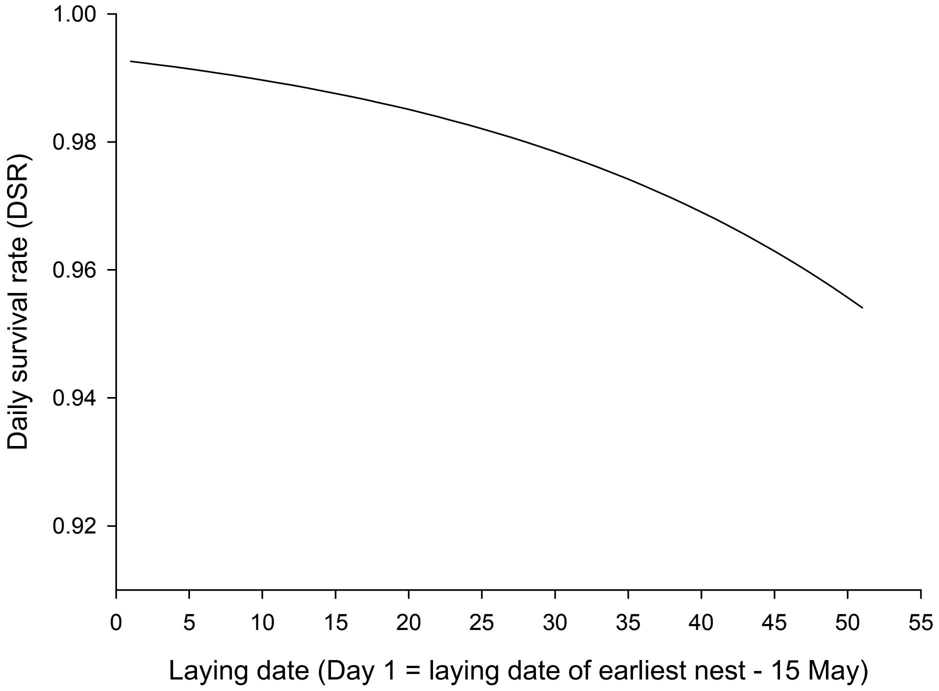


Figure 4.4 Daily survival rate (DSR) for red-throated diver estimated for the third best supported model with an individual effect of egg volume (model 3). The model uses egg and chick stage survival information.

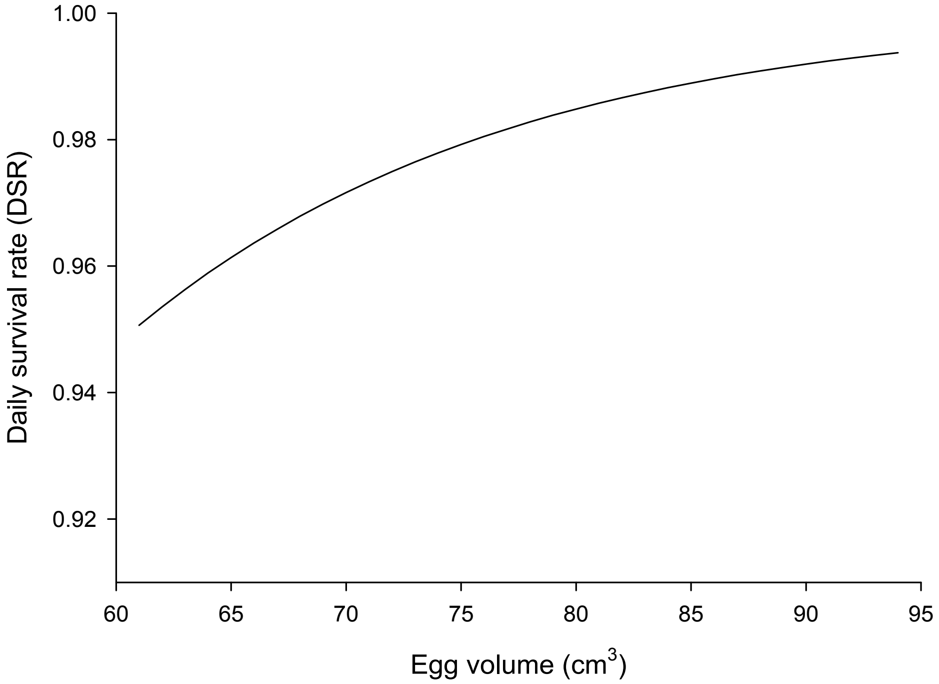
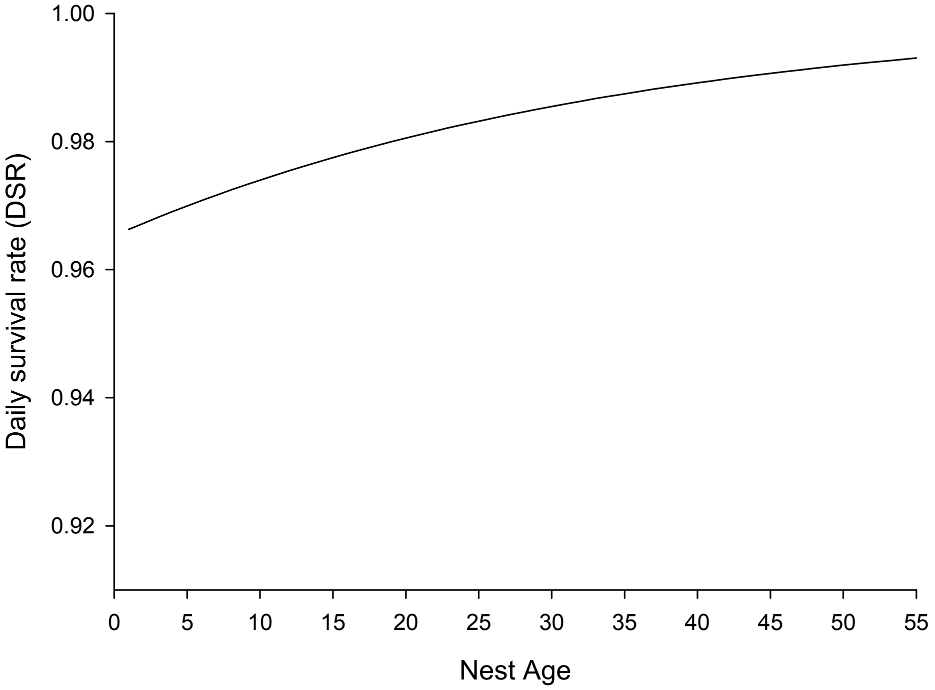


Figure 4.5 Daily survival rate (DSR) for red-throated diver estimated for the fourth best supported model with an individual effect of nest age (model 4). The model uses egg and chick stage survival information.



4.5 Discussion

Models with individual or additive effects of egg volume and laying date comprised the three best supported models. Fitted parameter estimates for the laying date model (model 2) indicated a gradual decrease in nest survival with laying date (Figure 4.3). The egg volume (model 3) indicated that nest survival increased with egg volume (Figure 4.4) suggesting that better quality birds also bred more successfully. Earlier breeders did not have significantly larger egg volumes per clutch but clutch size did decrease with laying date. Figure 4.2 shows the survival probabilities of the largest egg in the sample compared to the smallest under the constraints of the best model (model 1). It indicates that for high quality birds survival starts high and declines gradually whereas for low quality birds daily survival starts lower and declines much more rapidly. This suggests that early breeding is advantageous for all breeding pairs but may be particularly important for low quality pairs.

One egg clutches had lower egg volumes than two eggs clutches suggesting birds that laid these eggs were of lower quality. This was substantiated by the lower daily survival rate for one egg clutches. Furthermore there was a significant decrease in clutch size with laying date. This suggests that one-egg clutches were laid by lower quality birds and that one egg clutches were more likely later in the season. This may have been because lower quality birds laid later or because birds laying replacement clutches had depleted their nutritional resources during their first attempt and were unable to lay two eggs.

The model with a quadratic effect of laying date (model 6) was not supported, suggesting that the nest survival pattern was not curvilinear. I predicted that this type of pattern should be associated with a peak in food availability or minimal predation pressure at some point in the breeding cycle (hypothesis 2). Despite this, the peak number of nest initiations did correspond with high and relatively stable daily survival rates for high quality birds using the best supported model (Figure 4.1) Higher quality birds are also likely to be more experienced, older birds and therefore more able to track predation pressures and thus breed when predation risk was lowest . By contrast nest survival rate for lower quality birds at peak nest initiation shows a declining trend suggesting poorer quality birds did not assess this risk.

The analysis of egg and clutch size data from the overall sample found no significant differences between study years. This may suggest that the overall quality of females in the sample population over this period was stable. This is not surprising as egg size is likely to be partly determined by quality traits, both heritable and non-heritable, that are acquired over the lifetime of the individual. Thus short-term constraints on quality such as reduced food availability during a particular breeding season may not be detected in changes in the overall quality of females in the population, as expressed through egg size.

Nest age was the best supported model in Chapter 2 and indicated that nest survival increased with nest age either as a consequence of increased parental effort or as a consequence of poor quality pairs failing in the early egg stage. Nest age in this model set was also supported (Table 4.2, Figure 4.4). An increase in survival with nest age should have the effect of maintaining high survival rates as the laying period progresses for high quality birds if lower quality pairs failed early. This appears to be supported by the relatively stable daily nest survival rates for high quality pairs (Figure 4.2, solid line).

Overall these results suggest that early breeding improves survival probability but this benefit is short lived for lower quality birds, implying that individual quality is important for sustaining the overall reproductive output through the breeding season. Nutritional resources for breeding will be determined by food availability on arrival at the breeding grounds and stored body reserves accumulated on migration and in non-breeding areas (Nager 2006). As a consequence, changes in nest survival may result from changes in prey quality, composition and availability along migration routes or in wintering areas. This may be particularly important for red-throated divers. Winter surveys of UK inshore areas have found some of the highest counts of red-throated divers in areas with high levels of mercury and organochlorines (PCB) in fish (National Marine Monitoring Working Group 2004; Webb *et al.* 2006; Webb *et al.* 2009). These areas are also subject to offshore wind developments. Future research should aim to identify migration routes, staging and wintering areas for specific breeding populations, and examine the importance of prey availability and quality in these areas for determining subsequent breeding condition. Red-throated divers feed on a variety of fish species (Cramp & Simmons 1977) of differing nutritional quality. One of these, the sandeel, provides particularly high nutritional value (Hislop *et al.* 1991) but its abundance in the waters surrounding Shetland breeding areas is unpredictable (Goodlad & Napier 1997). In response to low sandeel availability, red-throated divers appear to utilise other fish of lower nutritional value, for example, Saithe (*Pollachius virens*) (S.Hulka, D.Okill pers. obs.). Future research aimed at assessing the effects of utilising different fish prey on the individual condition and nest survival would help to determine the importance of sandeels for the long-term health of the red-throated diver population on Shetland.

5 Effect of nest and breeding site characteristics on red-throated diver nest survival

5.1 Abstract

Birds are expected to select breeding sites to maximise their reproductive success. For ground nesting species in particular, predation is an important cause of nest failure and therefore breeding site location should minimise predation risk. However, for birds breeding in harsh environments, the choice of breeding site may be determined at least in part, by the need to provide optimal conditions for embryo and chick growth. In this study, I measure nest site and breeding site characteristics at three spatial scales; differentiate habitat characteristics that are likely to be related to microclimatic conditions and those which are more relevant to minimising predation risk and, by testing the effects of these characteristics on nest survival rate, assess the relative importance of predation risk and environmental conditions around the nest and at the breeding site. Characteristics related to predator avoidance and environmental conditions were both important in determining nest survival, however poor environmental conditions improved nest survival rate suggesting that their effect was to reduce the quality of predator foraging conditions and not to directly impose environmental constraints on nest survival.

5.2 Introduction

Birds are expected to select breeding sites that maximise their reproductive success. Predation is the principal cause of nest failure for many species typically accounting for *ca*. 50% of losses (Ricklefs 1969), and may also be a source of adult mortality at nests (Sargeant *et al*. 1984), thus breeding birds should minimise predation risk to eggs and offspring (Martin 1992; Sieving & Willson 1998; Forstmeier & Weiss 2004; Miller *et al*. 2007), while optimising their own survival chances (Lima & Dill 1990; Lima 1993) when selecting nest sites. Achieving this may involve a trade-off between a location where the nest is concealed from predators and one where visibility from the nest allows early detection of a predatory threat (Gotmark *et al*. 1995). For ground nesting species in particular, predators may develop a search image which improves their ability to locate nests (Greig-Smith 1982; Schieck & Hannon 1993) To counter this, birds may reduce cues to predators by nesting in vegetation types that do not differ from the vegetation in non-used locations (Storaas & Wegge 1987; Thompson *et al*. 1987; Schieck & Hannon 1993). Environmental conditions in the nest are important for embryo and chick development and survival (Webb 1987) and locating a nest to provide an optimal nest microclimate has been demonstrated to improve breeding success (Webb & King 1983). This may be of particular importance for open-nesting species or for those nesting in harsh environments (e.g. Wiebe & Martin 1998). Furthermore exposure to adverse environmental conditions may increase the physiological stresses on incubating adults and as result have consequences for nest survival. For example, (Goldstein 1983) found a linear increase in metabolic rate with increasing wind speed. Choosing a sheltered nest location therefore minimises the energy required to maintain body temperature. This may reduce the nutritional requirements for an incubating bird, reducing food intake and allowing higher nest attendance.

At a larger spatial scale breeding sites that have access to good foraging areas may be preferred (Brown & Brown 1996), as may the proximity to conspecifics as this may reduce the chances of predation and provide information about current food availability (Coulson 2002). Conversely territorial behaviour of conspecifics may render otherwise suitable breeding sites unavailable to prospecting birds (Fretwell & Lucas 1969).

Nest site preferences can evolve where habitat differences occur between successful and unsuccessful sites (Martin 1998), leading to preferences that are genetic, imprinted or learned (Klopfer 1963; Hilden 1965; Cink 1976; Sonerud 1985). Although these preferences are optimal over evolutionary time, short-term variation in selective pressures such food availability and predation risk may lead birds to select sites that are suboptimal, based on preferences derived as a consequence of natural selection (Clark & Shutler 1999). To maximise the value of nest site selection studies it is therefore necessary to identify differences between successful and unsuccessful sites as well as between selected and non-selected sites (Clark & Shutler 1999).

Red-throated divers are a ground nesting species breeding predominantly in arctic and subarctic areas. Typically, they nest in open locations on the shores or islets of freshwater ponds and lakes, foraging and provisioning young exclusively with fish caught away from the breeding lake (Cramp & Simmons 1977). Avian and mammalian predation have been identified as a principal proximate cause of breeding failure (Bundy 1976; Bergman & Derksen 1977; Gomersall 1986; Dickson 1993; Eberl & Picman 1993; Dahlén & Eriksson 2002) and this combined with frequent adverse weather conditions to which birds nesting at these latitudes are exposed, suggests that the choice of breeding site is likely to have important repercussions for egg, chick and adult survival. Previous studies (Lokki & Eklof 1984; Douglas & Reimchen 1988; Dickson 1993; Eberl & Picman 1993; Skyllberg *et al.* 1994; Dahlén & Eriksson 2002) have measured nest and breeding site characteristics at different spatial scales and compared them to levels of hatching and overall breeding success. At the nest-site scale these have included: vegetation height (Skyllberg *et al.* 1994); island nests (Lokki & Eklof 1984; Dahlén & Eriksson 2002); nest distance from the shore (Dahlén & Eriksson 2002);ambient temperature and rainfall during the breeding period (Dahlén & Eriksson 2002). At the 'breeding lake' scale: lake size (Bundy 1976; Gomersall 1986; Douglas & Reimchen 1988; Skyllberg *et al.* 1994; Eriksson & Johansson 1997; Dahlén & Eriksson 2002); proportion of emergent vegetation (Skyllberg *et al.* 1994); water flowing though lakes (in and out flow streams) (Dahlén & Eriksson 2002); and at the regional scale: distance to the nearest foraging waters (Eberl & Picman 1993); distance to nearest conspecific breeding lake (Gomersall 1986) and distance to nearest road (Gomersall 1986; Dahlén & Eriksson 2002) have been examined. Of these, locating nest sites amongst vegetation higher than 0.3m (Skyllberg *et al.* 1994); on lakes less than 1 hectare (Gomersall 1986), with more emergent vegetation (Skyllberg *et al.* 1994), with inflow and outflow streams (Dahlén & Eriksson 2002), or less than 9km from the nearest foraging areas (Eberl & Picman 1993) had positive effects on breeding success. In addition, higher temperatures and lower rainfall during the egg stage improved breeding performance while higher rainfall during the chick stage reduced it in one study (Dahlén & Eriksson 2002). Many of these characteristics have been tested at single study sites within habitat that are only partly representative of the range occupied by the species, however they do suggest red-throated divers maximise breeding success by selecting nest sites that both reduce predation risk and provide optimal environmental conditions for egg and chick development. The importance of characteristics to breeding success has typically been made using qualitative assessments based on the relative strength of correlations or chi squared tests between individual characteristics and breeding success measures, but no attempt has been made to distinguish between nest site preferences more formally. Assessing habitat requirements to inform species conservation planning is an important reason for investigating habitat preferences, and for this, nest survival measures rather than the breeding outcome measures used in these studies may be more appropriate (Jehle *et al.* 2004).

Here I use an information-theoretic model building approach (Burnham & Anderson 2002) implemented using the nest survival model in program MARK to evaluate the relative effect of habitat characteristics at different spatial scales on red-throated diver nest survival rates. I use the results to assess the relative importance of minimising predation risk compared with providing optimal environmental conditions at the nest in determining breeding site location.

I draw on the results of previous research examining red-throated diver breeding site selection and more general research examining the factors affecting avian breeding habitat selection, to develop a set of relevant hypotheses which I use to inform the building of a set of candidate models.

At the nest site scale I predict that:

1. Island nest sites reduce predation risk.

2. Nest sites positioned closer to the water edge, on lower banks or adjacent to deeper water minimise the chances of predator detection when incubating birds are leaving or arriving at the nest. Red-throated divers find it difficult to move on land and are conspicuous when they do so, thus a nest site that allows birds immediate access to the water is likely to minimise cues to predators.

3. Nests where the fetch orientation corresponds with the direction of the prevailing wind; or where the fetch distance to the nest is higher are

more exposed to the effects of the wind and hence, have lower daily survival rates.

4. The proportion of time that nest orientation corresponds with wind direction during the period when the breeding attempt is active is negatively related to nest survival.

5. Nest survival is not affected by the type of vegetation surrounding the nest because the vegetation is generally short and does not hide nests from predators. Given the exposed and predictable shoreline location of nests, I assume that adults minimise the chance of predators forming a search image of nest locations by choosing to nest in vegetation similar to the non nest shoreline vegetation.

6. Warmer, drier and less windy weather conditions during the period when the breeding attempt is active improves nest survival because; stresses on embryos and offspring associated with lower temperatures are minimised and adults require less energy for body maintenance and therefore need to forage less, allowing higher levels of nest attendance.

At the breeding lake scale I predict that:

7. Smaller lakes at higher elevations have higher nest survival because these lakes are likely to have a lower frequency of foraging predators.

8. Lakes without inflow or outflow streams have higher survival rates because they are less frequented by otters (*Lutra lutra*). Small streams are important as foraging habitat and corridors for otters (de Leaniz *et al*. 2006).

9. The proportion of time that the orientation of the longest axis of a lake corresponds with wind direction during the period when the breeding attempt is active is positively related to nest survival because it allows better take-off conditions. Adults require at least 15m to take-off (Norberg & Norberg 1971) and to obtain maximum uplift take off into a headwind, thus on small lakes in particular, a lack of wind along the

longest axis of the lake can prolong predator escape and potentially limit chick provisioning flights.

At the regional scale I predict that:

10. Distance to the nearest coastal foraging area does not affect nest survival, Sample sites were 1.14km ± 0.08 from the nearest coastal foraging. Based on a minimum flight speed 60km/hr (Norberg & Norberg 1971) this represents a flying time of *ca.* 1 minute and I therefore assumed that flight time to or from a coastal foraging area is unlikely to affect nest attendance.

11. Breeding sites with a neighbouring unoccupied lake available nearby have higher nest survival rates. Douglas and Reimchen (1988) found that these lakes provided an important predator escape. In addition off-duty birds often remain on a nearby lake when not foraging and this may allow increased predator vigilance as well as reducing the conspicuousness of the nesting lake (S.Hulka pers.obs.).

5.3 Methods

I monitored nest survival of red-throated divers nesting at 123 widely scattered lakes, in a 250 km^2 area of central Mainland Shetland, Scotland (60°35'N 01°25'W) during three breeding seasons (2006-8) (see Chapter 3, for details of nest survival monitoring procedures). I measured habitat characteristics at a random subsample of these lakes. The nest survival model in program MARK requires that timing of breeding is known for all nests, so the sample used in the analysis was determined by the presence of laying date information and habitat data (see Chapter 3, section 3.3.3, *Timing of breeding attempts,* for details of how laying date was determined).

Red-throated divers forage and provision young exclusively with fish caught away from the breeding lake, thus breeding site selection may involve decisions at spatial scales larger than that of the nest site or breeding lake. As well as the relative importance of individual characteristics I was interested in whether decisions at a particular spatial scale were more important. I defined three spatial scales potentially relevant to breeding site selection. These were; 1) the 'nest-site' scale, which included a) habitat features within 1m of the nest b) variables that had a spatial relationship to the nest site, for example the distance of open water between the nest and the opposite shore and c) environmental measures for the period when the nest was active, for example average rainfall 2) the 'breeding lake' scale, which included a) variables related to the morphology of the breeding lake, for example lake size and orientation and b) lake-specific environmental conditions (see below) 3) the 'regional scale' which included characteristics of the breeding lake in relation to other potentially relevant variables; for example, the distance to the nearest coastal foraging area.

At the ‘nest site’ scale, variables in a) were measured during field visits, those in b) measured from O. S 1:25000 maps and those in c) derived from weather data recorded at the meteorological station at Lerwick adjacent to the study site. At the 'breeding lake' and ‘regional’ scales, measurements were extracted from O.S. 1:25000 maps or derived from the Lerwick weather data record.

During licenced nest visits in 2006 and 2007 I photographed 1m^2 plots centred on each nest to record the composition of vegetation around the nest. In addition I photographed 1m^2 non-nest vegetation plots at 50m intervals along the shoreline of a random subsample of 18 breeding lakes to achieve a 2% photographic sample of vegetation within 1m of the shore to compare with the 1m^2 plot at the nest. To minimise disturbance to the breeding attempt I made an additional visit to the nest after egg stage was complete to measure; nest height above the lake water surface; distance from the water's edge to the centre of the nest (nest diameter for 34 clearly defined sample nests was very similar, averaging 0.30m, SD = 0.023 so I assumed using centre of the nest was a reliable point to measure from); and depth of water at the location where nesting adults entered or left the water when arriving or departing the nest. These measurements were rounded to the nearest 0.05m in the field. I categorised each nest as either positioned on the shore or on an island. Islands were surrounded by open water and a minimum of 1m from the shore. On O.S. 1:25,000 maps I pinpointed each nest location and measured the fetch distance and orientation from the nest to allow the possible effects of exposure of the nest to wave action to be assessed. Fetch orientation was the angle at 90 degrees to the average orientation of the shoreline at the nest. Fetch distance was the distance between the nest and the opposite shore or obstructing island along the line described by the fetch orientation angle. Fetch orientation and distance were rounded to the nearest 10° and 10m respectively. To further assess the possible effects of nest exposure to environmental conditions I obtained wind direction data for the study period, and calculated the number of hours that the wind direction corresponded to the fetch orientation (see below). I was not able to measure ambient temperature, wind speed or rainfall at individual nests, but to assess the effects of these factors on nest survival I calculated nest-specific averages (see below) using data from the weather station at Lerwick within 40 km of all sample study nests.

At the 'breeding lake' scale I measured area, elevation, orientation of the longest lake axis. Red-throated divers frequently breed on water bodies that are not recorded on O.S maps. For these, I took frequent GPS readings around the lake perimeter during field visits, downloaded these into DMAP® mapping software and used the 'map areas' component in that program to calculate the area. I used the lake shape described by the GPS readings presented in DMAP to identify the orientation and distance of the longest axis for these water bodies. If breeding lakes were mapped I used this information to measure these characteristics. I estimated elevation using the nearest 10m contour to the lake for those recorded on the map and the nearest contour to the GPS reading for the centre of the lake derived from the DMAP image for unmapped lakes.

At the 'regional scale' I measured the distance from the centre of each sample lake to the nearest; coastal water, metalled road and lake over 0.1 ha that was unoccupied during the three study years. I did not include adjacent water bodies under 0.1 ha because they are rarely used by breeding adults (S. Hulka. pers. obs.).

Vegetation surrounding the nest typically comprised; moss (*Sphagnum sp.*), moorland sedge and rushes (*Eriophorum sp./Juncus sp.*), and heather (*Calluna sp.*) either as the sole vegetation type or in varying proportions. From visual inspection of the nest photographs I estimated, to an approximate accuracy of 10%, the proportion of each of the three vegetation types within the 1m square centred on the nest. I then assigned each nest into one of seven categories based on dominant vegetation type/s. The categories were; 1) moss, 2) grass, 3) heather, 4) moss/grass, 5) moss/heather, 6) moss/grass, 7) moss/grass/heather. I used decision rules to assign categories: If the proportion of one vegetation type was double or more that of either of the other two types then it was singularly dominant (categories 1-3: e. g. 30% moss, 60% grass, 10% heather = category 2). If the proportions of two vegetation types were less than twice that of each other but both were double that of the third then I defined these two types as dominant (categories 4-6: e. g. 50% moss, 40% grass, 10% heather = category 4); if the proportion of any vegetation type was less than twice of any of the others I categorised none as dominant (category 7: e. g. 40% moss, 40% grass 20% heather = category 7). I applied these rules to categorise the vegetation type at each of the 1m^2 non-nest plots around selected breeding lakes. To allow the single nest vegetation plot to be compared with the multiple non-nest plots I used the modal category of the random plots at each lake.

To obtain an average air temperature, rainfall, and wind speed for each nest I averaged daily means over the period when the nest was 'active'. For successful pairs this was the period between the observed or estimated laying date and the date when at least one chick reached four weeks. For failed pairs this was the period between the laying date and the mid-point between the date last seen surviving and the date confirmed as failed. I grouped fetch orientation into four 90°categories; N to E, E to S, S to W and W to N, to obtain individual parameter estimates that could be tested against general measures of wind direction for overall study period. To calculate exposure of the nest to the wind I calculated the number of hours that the wind direction was within 10 degrees of the fetch orientation for the period that the nest was active and expressed this as a proportion of the total number of hours that the nest was active.

5.3.1 Statistical analysis

To determine whether vegetation in non-nest plots differed from nest plots I used Wilcoxon signed ranks test, and to distinguish differences in daily survival rate between different nest plot vegetation types I used unpaired t-tests with Welch's correction where variances were significantly different. To test for differences in nest survival rate between different fetch orientations I used one-way ANOVA followed by Tukey's multiple comparison tests. To test an earlier finding that smaller lakes had higher hatching success (Gomersall 1986) I used chi-squared tests. To examine the possibility that variation in certain habitat characteristics might be due to individual quality, I tested these against average egg volume measures taken at sample nests using one-way ANOVA or simple linear regression. Statistical tests were carried out using SPSS (SPSS Inc. version 15). All tests were two-tailed with the significance level set at $P = 0.05$. Summary statistics are presented as mean ± 1SE.

I used the nest survival model in program MARK (White & Burnham 1999) to evaluate the effect of nest and breeding site characteristics on daily nest survival rates (see Chapter 3,section 3.3.4, *Preparing survival data for Program MARK* for details of data preparation for nest survival modelling using MARK). The nest survival model in MARK assumes that nest fates are independent. At all spatial scales I restricted model building analysis to first breeding attempts because second breeding attempts occurred on the same lakes and may have involved one or both of the adults from the first attempt.

At the nest scale I evaluated 17 candidate models based on the *a priori* hypotheses (Table 5.2). First I fitted the nest survival data to a model where survival was held constant throughout the study period (model 6). Then I fitted each of the nest scale covariates individually to evaluate the influence of nest predation (models 1,4,8,11,12) and nest microclimate (models 2,3,7,9,10,) on nest survival. For rainfall, wind and temperature covariates I also tested for an effect of breeding stage (models, 5,14, 15,) to test whether average rainfall, wind and air temperature had different effects on nest survival at the egg and chick stage. I evaluated the model output that related to predation and microclimate separately and together. In addition to obtaining parameter estimates from the mean covariate values I ran models to obtain individual parameter estimates for each of the seven vegetation types and each of the four fetch orientation categories so that these could be compared with the dominant wind direction for the study overall. I ran a second analysis that tested the top model from the nest scale candidate set (model 1), against the top model from Chapter 3 testing variation in nest survival across the breeding cycle (model 18), and the top model from Chapter 4 evaluating the effect of date and individual quality on nest survival (model 19) (Table 5.3).

At the breeding site and regional scale, I first fitted the constant survival model (model 6), followed by each covariate individually (models 2-5 and 7-10). I then tested whether the additive effects of the two best individual models improved survival (model 1) (Table 5.4). I also compared the top model at these scales with top models from the breeding cycle (Chapter 3) and individual quality (Chapter 4) analyses (Table 5.5).

I used the default sine and logit link functions for constant survival and covariate models respectively (White & Burnham 1999). Competing models were ranked according to their respective Akaike's Information Criterion value (AICc) values and the model best supporting the data identified as that with the lowest (AICc) value. I used the associated Akaike weight (Wi) to quantify the degree of support between competing models and assumed that there was considerable support for a difference between two models if the Δ $AICC_c$ values differed by greater than 2. To examine the variation in daily survival rate (DSR) for specific models I used beta parameters and back-transformed these from the logit scale to obtain real parameter estimates.

5.4 Results

I recorded nest survival and obtained laying date information from 103 first attempts; 30 in 2006, 45 in 2007 and 28 in 2008. These were included in the MARK analysis of breeding site characteristics measured at the breeding lake and regional scales because this information was derived from maps or non site-specific weather data and was therefore available for all sites with survival information. The nest scale analysis was limited to the 42 breeding attempts where I had recorded nest site information during field visits in 2006 or 2007. A reduced dataset of 31 nests at the nest scale and 66 nests at the breeding lake/regional scales had all the measures required to compare top nest characteristic models with top models from breeding cycle and date and individual quality analyses (Chapters 3 and 4 respectively).

Sample nest sites were on the main shoreline of breeding lakes except for two that nested on islands. Nest scale sample nests were all less than 0.25m above the water level and less than 0.90m away from the water's edge, with a maximum depth of water at the 'nest run' of 1.10m. (Table 5.1 gives descriptive statistics for nest and breeding site characteristics that had either ordinal or scale measures) Of the 42 nests examined, most were located within vegetation that was either dominated by moorland grasses (Eriophorum sp) (17 nests) or a mix of moss (Sphagnum sp.) and moorland grasses (16 nests). Only six nests were in close proximity to vegetation containing heather. Typically nests had a fetch orientation that was north-east through to south-facing (IQR = 40 - 180°). The sample of 103 breeding lakes ranged in area from 0.01 to 20 ha but only 3 of these were greater than 2 ha, and 23 were less than 0.1 ha. Approximately half of all sample lakes had streams either entering or leaving. Elevation of breeding lakes ranged from 10m to 250m but the middle 50% of these were restricted to a 35m band between 80 - 115m. All sample breeding lakes were within a few minutes flight time (Norberg & Norberg 1971) from the nearest coastal waters and approximately one third, (31 lakes) within 500m of the nearest metalled road.

At the nest-scale, when factors potentially influencing both nest predation and microclimate around the nest were included, the best model included an effect of nest distance from the water's edge (model 1, Table 5.2). The predicted survival values fitted from the beta values for this model suggested that nest survival decreased with distance from the shoreline (Figure 5.1). This model was between *ca* 1.5 and 2.5 times better supported than three other models which had Δ AICC values less than 2. These were models with effects of average wind speed (model 2) and average rainfall (model 3) during the period when nests were active, and a model with an effect of nest height above the water (model 4). Predictions based on the beta values for these models suggested that nest survival increased with wind speed (Figure 5.2) and rainfall (Figure 5 3). The 95% confidence interval for the nest height model overlapped zero suggesting little variation in survival with nest height. When I grouped models into characteristics that were predicted to affect nest survival by altering predation risk (models 1,4,8,11,12) and those that were expected to affect nest microclimate (models 2,3,7,9,10) the two best supported models were nest distance (model 1) and average wind speed during the period that the nest was active (model 3). Models that included an effect of vegetation type (model 8), water depth at the run to the nest (model 11) or island or shoreline location (model 12), were also predicted to influence nest survival by altering predation risk but received no support. Additionally models that tested the effect of fetch orientation, fetch distance, air temperature and nest exposure, were expected to influence nest survival by altering microclimate at the nest site but were also unsupported. Adding breeding stage to average wind speed (model 15), rainfall (model 5), air temperature (model 14) and exposure (model 16) resulted in models that were all unsupported by the data. To examine possible effects of individual quality on the nest distance model I regressed egg volume for those nests where this information was available against nest distance and found that average egg volume decreased significantly with increasing nest distance from the shore ($F_{1,30}$ = 5.24, P = 0.03, $R^2_{ad\ j}$= 0.12).

The majority of the 42 sample nests were located amongst vegetation that was dominated by grass only (16 nests) or a mixture of moss and grass(17 nests) with slightly higher daily survival rates higher for nests amongst grass (0.993, SE = 0.003, N = 17) compared with those within a mixture of moss and grass (0.982, t_1 = 1.62, P = 0.12). I found no difference between categories assigned to the 1m^2 nest vegetation plots and non-nest vegetation plots sampled around the same breeding lake (Wilcoxon signed ranks test; Z = -6.73, N = 18, P = 0.51). Nests with a fetch orientated toward the north-east (0 - 90°) had marginally higher nest survival rate than nests in any of the other three orientation categories. These differences were not significant (one-way ANOVA: $F_{3,29}$ = 0.419, P = 0.74) but the sample sizes for the south-east, south-west and north-west quadrants were small and thus reduced the power of the test. Egg volume was on average greater for nests with a fetch orientation within the north-east quadrant (80.28cm^3, SE = 1.74, N = 15) than for nests in any of the other 3 quadrants (76.03cm^3, SE = 2.54, N = 8; 76.51cm^3, SE = 4.57, N = 5; and 75.80cm^3, SE = 1.59, N = 5 for south-east, south-west and north-west quadrants respectively) but there were no significant differences between the groups (one-way ANOVA: : F_3 = 0.953, P = 0.43.

At the breeding lake and regional scale, an effect that measured the proportion of time that wind direction corresponded with the longest axis of the breeding lake and a model with an effect of elevation were the two top individual models (models 2 and 3 respectively, Table. 5.4) Nest survival rates predicted from the beta coefficients for each of these models suggested that nest survival decreased as wind along the long axis of the lake increased (Figure 5.4) and increased as elevation increased (Figure 5.5). Adding the effect of elevation to the wind/lake orientation model gave the best supported model at the breeding lake or regional scale (model 1, Figure 5.6). Using the beta values from model 1 to predict nest survival for hypothetical nest at 10m a.s.l and one at 250m a.s.l. indicated that nest survival at higher altitude lakes was higher and decreased less as lake orientation/wind direction increased compared with low attitude lakes .Nests at higher lakes also had larger mean clutch volumes (78.99cm^3, SE = 1.18, N = 31 for nests between 110 and 190m) compared with those at lower elevations (77.12cm^3, SE = 0.69, N = 65, for nests between 20 and 100m), however the difference was not significant t_{94} = 1.45, P = 0.15).

Gomersall (1986) found that pairs that bred on water bodies under 1 hectare had significantly better hatching success. There was no support for the model with an effect of breeding lake area on nest survival and the egg stage survival rate for small lakes of less than 1 hectare was only slightly higher (0.987, SE = 0.003, N = 82) than that of larger lakes greater than a hectare (0.973, SE = 0.009, t_{101} = 1.68, P = 0.10). There was also no difference in average egg volume between the smaller (78.35cm^{3,} SE = 0.99, N = 50) and larger lakes (77.53cm^3, SE = 0.89, t_{64} = 0.45, P = 0.65). Lakes under 1 hectare did have higher hatching success compared with larger lakes but with only borderline significance (χ^2_1 = 4.21, P = 0.052). The majority of red-throated diver breeding lakes are smaller than 1 hectare and this was represented in my sample. I therefore tested for differences in hatching and overall success above and below the median lake size for this sample (0.3 ha). Hatching success for lakes smaller than 0.3 hectares was significantly higher than for lakes above the median size (χ^2_1 = 6.68, P = 0.01), but interestingly there was no significant difference in overall success between these lake size categories. (χ^2_1 = 2.84, P = 0.11).

The best models from the analysis of nest survival variation through the breeding cycle (Chapter 3) and nest survival in relation to date and individual quality (Chapter 4) had an effect of nest age (model 18) and an additive effect of laying date and egg volume (model 19) respectively. When these models were evaluated against the best supported nest distance model in the nest scale analysis, nest distance was the only supported model (Table 5.3). Similarly at the larger spatial scales, the best supported model from the habitat analysis, with an additive effect of elevation and proportion of time that the wind direction corresponded with lake orientation received substantial support but nest age and the model with additive effects of laying date and egg volume were unsupported (Table 5.5).

Table 5.1 Descriptive statistics for red-throated diver breeding site characteristics analysed in program MARK.

	Characteristic	*N*	Mean	±SE	Range
Nest	Nest height above water level (m)	42	0.12	0.01	0 - 0.25
	Nest distance from water's edge (m)	42	0.44	0.03	0.15 - 0.90
	Water depth at run to nest (m)	42	0.31	0.04	0.05 - 1.10
	Fetch distance from nest to opposite shore (m)	42	55.48	0.06	10 - 190
	Fetch orientation from nest to opposite shore (°)	42	114.85	15.68	0 - 350
	Proportion of time fetch and wind direction equal (exposure)	42	0.11	0.02	0.02 - 0.44
	Average wind speed for period when nest was active (knots)	42	11.64	0.13	8.89 - 12.75
	Average temperature for period when nest was active (°C)	42	11.14	0.14	8.92 - 13.38
	Average rainfall for period when nest was active (mm)	42	1.94	0.14	0.26 - 3.59
Breeding lake	Lake area (ha)	103	0.82	0.21	0.01 - 19.9
	Elevation (m)	103	101.17	4.35	10 - 250
	Lake orientation (°)	103	93.4	5.83	0 - 180
Regional	Distance to nearest metalled road (km)	103	0.95	0.06	0.06 - 2.57
	Distance to nearest adjacent lake over 0.1ha (km)	103	0.59	0.06	0.03 - 2.35
	Distance to the nearest coastal water (km)	103	1.14	0.08	0.15 - 3.85

Table 5.2 Model selection results for the effects of nest site scale variables on red-throated diver nest survival, Mainland Shetland, Scotland, 2006-8. AIC_C = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of $\Delta AIC_{c;}$ values. The intercept model assumes constant survival.

Model No.	Model	Deviance	Parameters	AIC_c	Δ AIC_c	AIC_c Weight (w_i)
1	Nest distance from shore (m)	90.46	2	94.47	0.00	0.27
2	Average windspeed (knots)	91.30	2	95.31	0.85	0.18
3	Average rainfall (mm)	91.99	2	96.00	1.53	0.13
4	Nest height above water	92.37	2	96.38	1.92	0.10
5	Breeding stage + rainfall (mm)	91.18	3	97.20	2.73	0.07
6	Intercept	95.91	1	97.91	3.45	0.05
7	Average air temperature (°C)	94.88	2	98.89	4.43	0.03
8	Vegetation type	94.99	2	99.00	4.53	0.03
9	Fetch distance	95.47	2	99.48	5.01	0.02
10	Exposure	95.50	2	99.51	5.04	0.02
11	Water depth	95.80	2	99.81	5.34	0.02
12	Island or shore nest	95.90	2	99.91	5.45	0.02
13	Breeding stage	95.91	2	99.92	5.45	0.02
14	Breeding stage + temperature	94.11	3	100.13	5.66	0.02
15	Breeding stage + wind speed	95.19	3	101.21	6.75	0.01
16	Breeding stage + exposure	95.49	3	101.51	7.05	0.01
17	Breeding stage + fetch direction	94.97	4	103.01	8.54	0.00

Table 5.3 Model selection results comparing the best supported model at the nest site scale; best supported model from the variation through the breeding cycle analysis (Chapter 3, nest age model) and best supported model from the effects of date and individual quality nest survival analysis (Chapter 4, laying date + egg volume model). AIC_C = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of $\Delta AIC_{c;}$ values. The intercept model assumes survival is constant.

Model No.	Model	Deviance	Parameters	AIC_c	Δ AIC_c	AIC_c Weight (w_i)
1	Nest distance from shore (m)	69.45	2	73.47	0.00	0.57
6	Intercept	73.57	1	73.57	2.11	0.20
18	Nest age	72.50	2	76.52	3.05	0.13
19	Laying date + egg volume	70.96	3	76.99	3.52	0.10

Table 5.4 Model selection results for the effects of breeding lake and regional scale characteristics on red-throated diver nest survival, Mainland Shetland, Scotland, 2006-8. AIC_C = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of $\Delta AIC_{c;}$ values. The intercept model assumes survival is constant.

Model No.	Model	Deviance	Parameters	AIC_c	Δ AIC_c	AIC_c Weight (w_i)
1	Lake axis/wind direction + elevation	238.15	3	244.16	0.00	0.33
2	Lake axis/wind direction	240.83	2	244.83	0.67	0.23
3	Elevation	241.99	2	246.00	1.84	0.13
4	Inflow or outflow streams	242.81	2	246.81	2.66	0.09
5	Nearest lake (>0.1ha)	242.95	2	246.95	79	0.08
6	Intercept	245.88	1	247.88	3.72	0.05
7	Lake axis	245.34	2	249.34	5.19	0.02
8	Nearest coast distance	245.48	2	249.48	5.32	0.02
9	Nearest road distance	245.63	2	249.64	5.48	0.02
10	Lake area	245.85	2	249.85	5.69	0.02

Table 5.5 Model selection results comparing the best supported model at the breeding lake scale; best supported model from the variation through the breeding cycle analysis (Chapter 3,nest age model) and best supported model from the effects of date and individual quality nest survival analysis (Chapter 4, laying date + egg volume model). AIC_C = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of $\Delta AIC_{c;}$ values. The intercept model assumes survival is constant.

Model No.	Model	Deviance	Parameters	AIC_c	Δ AIC_c	AIC_c Weight (w_i)
1	Lake axis/wind direction + elevation	151.59	3	157.60	0.00	0.83
19	Nest age	155.39	3	161.40	3.80	0.12
18	Laying date + egg volume	159.58	2	163.59	5.99	0.04
6	Intercept	164.46	1	166.46	8.86	0.01

Figure 5.1 Daily survival rates (DSR) for red-throated diver estimated for the best supported model at the nest site scale with an effect of nest distance from the water's edge (model 1). The model uses egg and chick stage survival information.

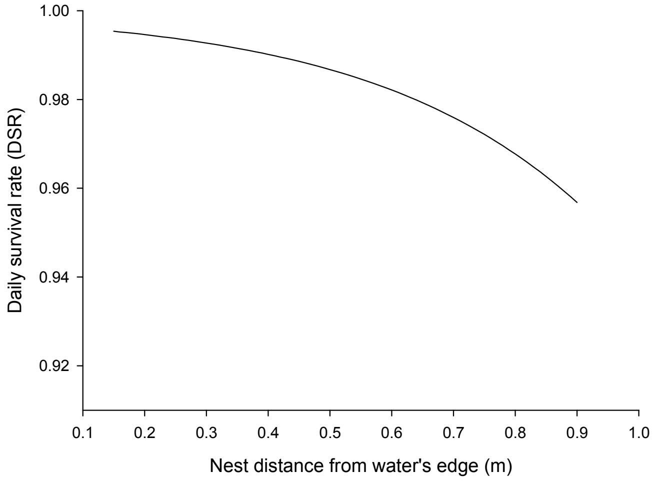


Figure 5.2 Daily survival rates (DSR) for red-throated diver estimated for the second best supported model at the nest site scale with an effect of average daily windspeed for the period when the nest was active (model 2). The model uses egg and chick stage survival information.

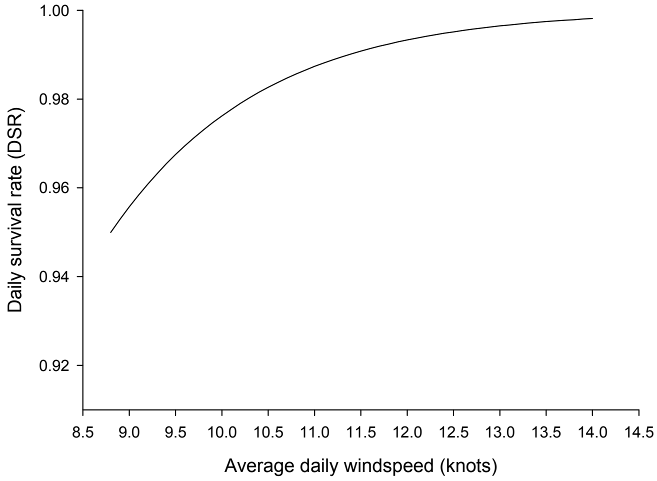


Figure 5.3 Daily survival rates (DSR) for red-throated diver estimated for the third best supported model at the nest site scale with an effect of daily average rainfall for the period when the nest was active (model 3). The model uses egg and chick stage survival information.

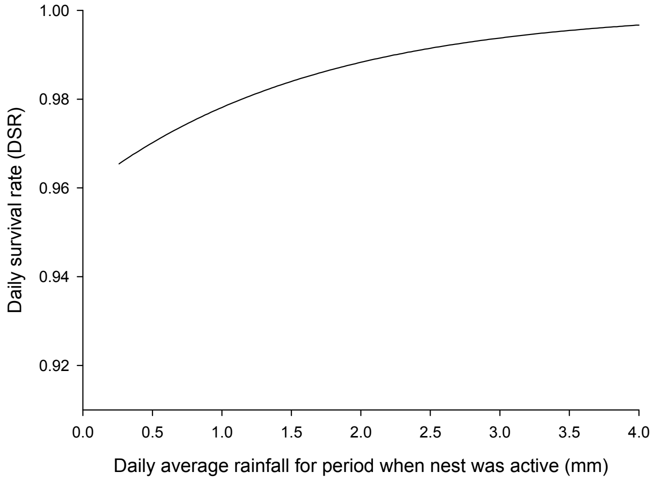


Figure 5.4 Daily survival rate (DSR) for red-throated diver estimated for the second best supported model at the breeding lake and regional scales with an effect of the proportion of time that wind direction was corresponded with the longest axis of the lake (model 2). The model uses egg and chick stage survival information.

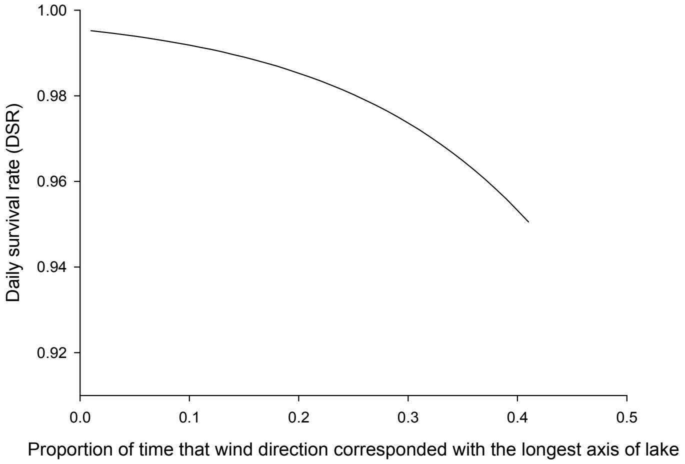


Figure 5.5 Daily survival rate (DSR) for red-throated diver estimated for the third best supported model at the breeding lake and regional scales with an effect of breeding lake height above sea level (model 3). The model uses egg and chick stage survival information.

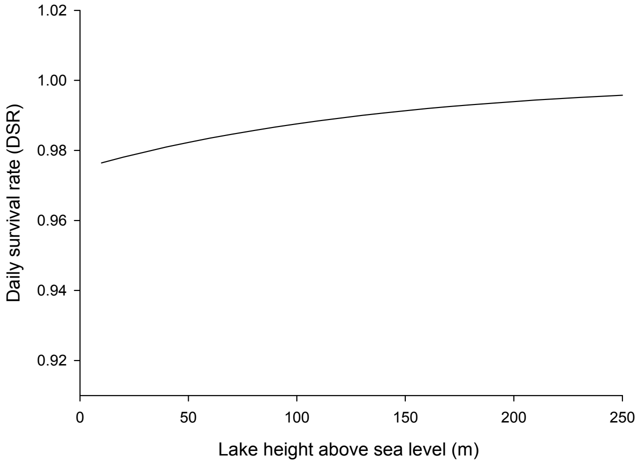
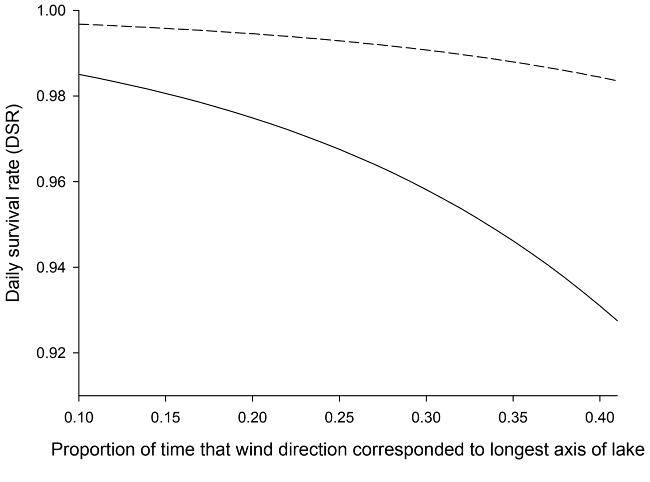


Figure 5.6 Daily survival rates (DSR) for red-throated diver estimated for the best supported model at the breeding lake and regional scales with an additive effect of the proportion of time that wind direction corresponded with the longest axis of the lake and lake elevation (model 2). Solid line represents a hypothetical nest at 10m a.s.l. and the dotted line a nest at 250m a.s.l.The model uses egg and chick stage survival information.



5.5 Discussion

Habitat characteristics affect red-throated diver daily nest survival rate at the nest-site and breeding lake scales, and these effects suggest that pairs that are able to secure nests sites and breeding lakes that minimise predation risk have better survival prospects. Regional scale characteristics were not supported in the MARK analysis. Compared with the effects of nest age and individual quality, the effect of breeding site choice appeared to be more important. However, comparing the habitat characteristics of the best models with egg volume as an index of individual quality indicated that breeding site selection and individual quality were related.

The best model at the nest scale indicated that nest survival was reduced for nest sites located further from the water's edge (model 1). Red-throated divers are not suited to movement on land and do so in a series of conspicuous lunges, thus nests further away from the water are more likely to be detected, particularly by avian predators that may use vantage points to detect prey. Conversely nests located next to the water’s edge allows incubating or brooding birds to arrive and leave the nest cryptically and thus reduce predation risk. I assumed that nest located on lower banks would improve nest survival for the same reason, but found less support for the model with an effect of nest height above the water (model 4). This may suggest that avoiding detection when leaving or arriving at the nest only partly explained the support for the nest distance model. Hatching success is related to nest site breeding skills and increases with experience (Nelson 1966; Ollason & Dunnet 1978; Pyle *et al.* 1991) and it has been demonstrated that younger, less experienced birds lay smaller eggs than mature birds (Hipfner *et al.* 1997; Massaro *et al.* 2002; Bogdanova *et al.* 2006). There was a significant reduction in egg size with nest distance suggesting that younger and/or birds of lower quality were locating nests away from the shore. If this is the case then what is the perceived survival benefit to inexperienced birds? Flooding of nests is an obvious, frequently cited, and based on the evidence of previous work and of this study, a relatively unimportant threat to survival of red-throated diver nests (Dickson 1993; Eberl & Picman 1993; Dahlén & Eriksson 2002). One possible reason for inexperienced birds locating nests away from the shore could be that they erroneously perceive the threat of nest flooding above that of detection by predators.

Average wind speed and rainfall during the period when the nest was active (models 2 and 3 respectively) were positively related to nest survival, indicating that these environmental factors were important but probably not because of any direct consequence of their effects on microclimatic conditions in the vicinity of the nest. In Chapter 4 I found an effect of laying date on nest survival and average daily rainfall and wind speed may also vary with seasonal date leading to a confounding effect on nest survival. I found no correlation between daily wind speed and date of the season in any of the three study years suggesting that the wind speed model was not affected by a confounding effect of date. Rainfall and date was positively correlated in 2007 only (Spearman rank correlation; $r = 0.20$, $P = 0.03$), but because nest survival rate appears to decrease with laying date (Chapter 4, Figure 4.2), it seems unlikely that the effect of date on rainfall was confounding the nest survival pattern in the rainfall model (model 3). Improved nest survival with increasingly poor weather could have resulted if these conditions reduced foraging rates and/or predation rates of predators such as gulls and skuas that target red-throated diver eggs and chicks. Reduced foraging by some raptors during rainfall and in windy conditions has been demonstrated (Elliott *et al.* 2006), and Votier *et al.* (2004) found that in one breeding season characterised by very high rainfall, Great Skua (*Stercorarius skua*) foraging rates at one Shetland study site were relatively high, however poor food availability was also likely to have affected foraging rate here. Fog is frequently associated with poor weather conditions on Shetland. This is likely to reduce predator foraging efficiency and may have contributed to the pattern of increased survival in wetter, windier conditions. Although red-throated diver chicks typically leave the nest within 24 hours of hatching (Bundy 1976) they continue to be brooded for up to approximately two weeks. Brooding has been demonstrated to increase during rainfall and windy conditions for at least one precocial waterbird species (Mendenhall 1979) and this type of behaviour should reduce predation risk because chicks are underneath parents during these periods and as a consequence their survival probabilities are improved. The lack of support for models with an effect of fetch distance (model 9), fetch orientation (model 17)and the proportion of time that fetch orientation corresponded with wind direction (model 10) further suggests that microclimatic conditions at the nest site were a relatively unimportant determinant of nest survival. Nest survival was higher for nests facing north-east but this was not explained by the proportion of time that the wind was in each 90°quadrant for the 2006/2007 study seasons overall which was very similar (average = 0.25, SE = 0.03). This suggests that the positioning of nests sites was unlikely to be a direct response to topical conditions at the time of nest initiation. Historical data show that the prevailing wind between 1921and 2001 was south-westerly (Harrison & Nicoll 2008). The trend for nests to face north-east away from the long-term prevailing wind direction may suggest that contrary to the findings of this study, over evolutionary time natural selection has selected for nest sites to minimise exposure to adverse weather conditions. Average egg volume was also highest for nests facing north-east suggesting that higher quality birds occupied these sites. Analysing this type of data with larger sample sizes for each orientation category is needed to confirm this. Enquist (1983) found that Arctic skua *(Stercorarius parasiticus)* employ landscape features, memorise nest sites and make regular visits to red-throated diver nest sites to check on attendance. In other species breeding adults may reduce the cues to predators by nesting in vegetation types that do not differ from the vegetation in non-used locations (Storaas & Wegge 1987; Thompson *et al*. 1987; Schieck & Hannon 1993). Red-throated divers located nests in vegetation that was similar to the vegetation in the non-nest vegetation plots. Only two lakes were represented by a single vegetation category so breeding birds did have some choice regarding which vegetation to locate their nest. These general results may suggest that red-throated divers are not targeting particular vegetation types when locating nest sites, however, more detailed analysis of shoreline vegetation at nest sites and along the ribbon of shoreline suitable for nesting is required to confirm this, as well as experimental work to establish whether this initial result was a consequence of a decision to reduce predation risk by predators capable of memorising nest locations or coincidental to some other nest site location constraint. Red-throated divers, especially those that occupy established breeding lakes may use the same nest over many years. For these birds any attempt to reduce cues to predators appears to be either unimportant or outweighed by other factors.

At the breeding lake scale the best supported model comprised additive effects of elevation and the proportion of time that wind direction corresponded with the longest axis of the breeding lake, and graphing the effect of these factors on nest survival suggested that for lakes at both high and low elevations nest survival decreased with an increase in the proportion of time that the wind direction corresponded with the longest lake axis orientation. Red-throated divers require a minimum of 15m of water to take-off (Norberg & Norberg 1971), often have difficulty in doing so in calm conditions and prefer to take off into a headwind (S.Hulka pers.obs.). This result was therefore unexpected. I also tested this effect for small lakes because it seemed likely that these constraints may only effect nest survival when take-off was severely restricted however excluding all lakes greater than 0.3 ha from the analysis reduced support for this model. Alternatively this measure may describe increasing rough water conditions. This may reduce nest survival because it reduces adult vigilance of chicks. Testing the effect of lake orientation and wind direction for lakes at high and low elevation revealed that the fall off in nest survival was most pronounced for lakes at lower elevations. Lakes below the average elevation for the sample were similar in size to those above it (0.98 ha compared with 0.76ha respectively) and therefore fetch distances and wave action were probably similar. In the absence of a clear reason for this pattern it is likely that another factor that varied with elevation affected nest survival. One possibility is that prey items for predators were more abundant at lower elevations and this increased predation risk in these areas.

Gomersall (1986) found that nesting on small water bodies less than 1 hectare resulted in higher hatching success. I found no significant difference in nest survival or hatching success between these lake size categories, nor was there any difference in egg volume between the two groups, indicating that birds in better quality were not occupying smaller water bodies. Hatching success, but not overall success was higher at lakes below the sample median size of 0.3 hectares. In the core study area 10% of sites had breeding attempts that moved chicks to larger lakes soon after hatching. All these sites were less than 0.1 hectares, indicating that small lakes have some survival disadvantage during chick rearing. Red-throated divers nest in open, predictable locations, along the ribbon of lake shore, thus concealment from predators during incubation is likely to be primarily important, and very small lakes are often well concealed with few related topographical features such as streams that might attract predators. Chicks are able leave the nest soon after hatching thus the probability of survival is enhanced if escape options are maximised and larger lakes provide more escape options. Higher egg stage success combined with a lack of significant overall success at smaller lakes in this study suggest that pairs that use these lakes minimise predation risk and the availability of these smaller lakes is likely to be important for maintaining red-throated diver population health.

Gomersall (1986) also found no relationship between breeding success and distance to the nearest metalled road and using the same metric I found no support for a nest survival model with this effect (Table 5.4,model 9). This measure however takes no account of the type or frequency of traffic or visibility of the road from the breeding lake. Assessing the disturbance effect of a single nest visit for this study found no negative effect on fledging success ($\chi^2_1 = 1.02$, $P = 0.355$). This suggests that any disturbance effects are likely to relate to the frequency of disturbances rather than a single disturbance event. The support for an effect of nest age in Chapter 3 suggests that vulnerability to disturbance may decrease with increasing nest age. Furthermore eavesdropping on heterospecifics that are subject to the same predatory risks to obtain information about current threat levels has been demonstrated for some bird species (Hurd 1996; Shriner.W.M. 1998; Goodale & Kotagama 2008). Red-throated divers frequently breed on lakes occupied by heterospecifics, including potential avian predators such as gulls, and skuas and appear to make use of their alarm calls to inform escape decisions in relation to predators (S.Hulka pers.obs.) This is unsurprising as their view of the surrounding landscape is limited. Finally distinguishing the effects on survival of habituation to disturbance needs to be considered. Future studies should avoid using simple criteria to evaluate red-throated diver nest disturbance and should focus on dedicated research aimed at determining which disturbance factors are important and then distinguishing between them.

Eberl and Picman (1993) found that success was higher for pairs breeding less than 9km from the nearest foraging areas. In this study, the effect of nearest coastal distance on nest survival rate was unsupported. This is unsurprising as breeding sites were on average only 1km from the nearest coastal foraging and thus reduced vigilance attributable to flight time to and from breeding lakes was likely to be minimal. A model examining an effect of the length of time that individuals spend away from the breeding lake may better reflect the effect on nest survival of reduced off-duty vigilance, however any such measure needs to take account of vigilance by off-duty parents from an adjacent lake (S. Hulka pers. obs.).

The results of this study suggest that red-throated diver nest survival is maximised when pairs select nest sites that minimise predation risk. There was little evidence to suggest that nest survival was depressed by environmental factors creating a suboptimal environment at the nest site but nest-specific monitoring of thermal changes at each nest are needed to confirm this initial finding. Where environmental factors were important, such as improved survival associated with increased wind and rain, their survival benefits were likely to relate to reducing predation risk either directly by limiting predator foraging or indirectly by instigating higher levels of nest attendance. A relationship between breeding site preferences and individual quality was detected and understanding the relative importance of these two factors may be important when allocating conservation resources for the species. To do this effectively requires nest survival monitoring of individually identified breeding birds for which information on age, individual nutritional quality and nest site preferences are also available. Additionally, information on genetic relatedness of individuals in the study population may be useful for assessing heritable quality. Previous methods for identifying individual red-throated divers between years has been limited to the use of coloured leg-tags which, although effective, requires capture, and are only visible when the bird is in flight. Similarly, assessing nutritional quality has focused on body mass or morphometric measures (Okill & Wanless 1990) which require annual capture of study birds. Future research in this area should initially focus on developing and making use of novel, less invasive methods of identifying and measuring quality of individuals. For example, DNA sampled from hatched or predated eggshell and from feathers found at nests has a demonstrated validity for use in population genetic research (Pearce *et al.* 1997; Trimbos *et al.* 2009). Preliminary observations during this study suggest that egg membrane fragments are recoverable from many hatched nests and are always present attached to predated eggs. Shed adult feathers are occasionally found in nests, but to make effective use of this material a novel technique of obtaining a feather sample from incubating birds would be needed. Passive integrated transponder (PIT) tags incorporated into standard metal leg rings have been used to identify nesting individuals for dispersal, recruitment and site fidelity studies (e.g. Wright 2003) and although requiring initial capture, once attached can provide nesting location information for the breeding lifetime of the individual.

6 The effect of nest temperature and nest attentiveness on red-throated diver nest survival

6.1 Abstract

In an open nesting species, especially one that breeds in cool environments, the maintenance of nest temperature as close as possible to the optimum for embryo development may have benefits that are conferred to the offspring. However, the high levels of nest attendance required to achieve this may have fitness consequences for adults in terms of reduced foraging time and maintenance costs. Additionally, the duration and frequency of incubation recesses will affect mean egg temperature and may also have effects on predation risk. Here I test the effect of nest temperature, recess length and duration on nest survival probabilities. Nest temperature and the number of incubation recesses were not related to nest survival and the best supported model was the intercept model that assumed constant survival. There were clear patterns in activity through the day with the majority of recesses occurring away from the middle part of the day.

6.2 Introduction

Life history theory states that increased investment in limited resources during one life history stage must be compensated for with reduced investment in subsequent stages either within the same or in subsequent reproductive attempts (Stearns 1992). In birds, investment in a reproductive attempt is divided between egg laying, incubation and chick rearing stages, but most research has focused on the obvious demands of chick-rearing and its repercussions resulting from high resource allocation at this breeding stage (Monaghan & Nager 1997). Recent experimental studies have demonstrated that incubation demands can limit reproductive success, and resources conserved at this stage can be reallocated to later stages of the same breeding attempt (Heaney & Monaghan 1996; Reid *et al.* 1999; Hanssen *et al.* 2005). These demands include maintaining eggs in optimal conditions for developing embryos (Thomson *et al.* 1998; Bryan & Bryant 1999; Reid *et al.* 1999) and minimising the risk of egg predation, an important cause of breeding failure in many birds (Ricklefs 1969). Furthermore incubation demand will also limit the time available for other activities such as foraging, and for males to seek additional mating opportunities (Reid *et al.* 2002). Maintaining the optimum conditions for embryo development may be particularly important for precocial species whose morphological development is largely restricted to the egg stage (see Metcalfe & Monaghan 2001). Levels and patterns of nest attentiveness are likely to be an important factor influencing nest temperature and for understanding patterns of predation risk (Weathers & Sullivan 1989; Wilson & Verbeek 1995). Furthermore, high levels of nest attentiveness have been demonstrated to be positively related to body mass at the onset of incubation (Afton & Paulus 1992); increasing age (Aldrich & Raveling 1983); and better body condition (Gatti 1983).

Red-throated divers are precocial with biparental incubation averaging 27 days (range; 24 - 29 d, Bundy 1976; Cramp & Simmons 1977) during which eggs are covered more or less continuously. Incubation recesses occur in response to the presence of predators, disturbance, or pair-bond strengthening at, or away from the breeding lake (Cramp & Simmons 1977). Recesses may also occur when birds in poor body condition are forced to leave the nests to forage before the non-attendant partner returns (e.g. Bijleveld & Mullers 2009). Nests are typically located in short vegetation in open locations. Unattended eggs are therefore exposed to the effects of extreme temperatures and to visually searching predators. Nest predation is an important proximate cause of red-throated diver breeding failure (Bundy 1976; Bergman & Derksen 1977; Gomersall 1986; Dickson 1993; Eberl & Picman 1993; Dahlén & Eriksson 2002). Moreover, their circumpolar breeding distribution imposes time constraints on breeding more than once in a season because of limits on the time that breeding lakes are ice free (see Eberl & Picman 1993) and this may increase the importance of the initial breeding attempt. These vulnerabilities and constraints should exert a strong selective pressure for high levels of nest attendance and suggest that reduced attendance will have important fitness consequences.

Red-throated diver nest survival appears to increase with nest age (Chapter 3) and with individual quality as assessed using average clutch volume (Chapter 4). I was therefore interested to know if increased nest attendance through the incubation period and in relation to egg size reflected this.

In this study, I first calculate and describe red-throated diver nest temperature characteristics and describe recess frequency and duration through the day and in relation to nest age. Second, I use an information-theoretic model building approach (Burnham & Anderson 2002) implemented using the nest survival model in program MARK (White & Burnham 1999) to evaluate the effect of nest temperature and the number and duration of recesses on daily nest survival rates to test three hypotheses relating to underlying behavioural and environmental factors potentially affecting nest survival. Specifically I predict that:

1. Higher average nest temperatures are associated with higher daily nest survival rates because they reflect conditions closest to the optimal conditions for embryo development (Webb 1987).

2. More frequent recesses are related to lower daily nest survival rates because increased frequency of nest visits increases conspicuousness of the nest to predators.

3. Longer recess durations are related to lower daily nest survival rates because eggs are exposed to suboptimal conditions and risk of predation for longer.

Third, I test whether nest temperature and nest attentiveness is related to individual quality as estimated from average clutch volume and breeding outcome.

6.3 Methods

I collected nest survival information, and used temperature data loggers to measure nest temperature and collect nest attendance information during monitoring of 123 breeding lakes during three breeding seasons (2006-8) on Mainland Shetland, Scotland, as part of wider research on red-throated diver breeding biology. During the egg laying period, extending from early May to late July (Bundy 1976; Gomersall 1986; Natural Research unpubl. data), I made 100% shoreline searches to confirm breeding and determine nest fate (see Chapter 3 for a detailed description of search methods and criteria for confirming breeding and determining nest fate). Where incubation was proven I made a licensed nest visit to measure egg float angles (Westerkov 1950) and install temperature data loggers in the base of nests. During the chick-rearing period between late June and mid August I made follow-up visits to these sites to photograph relative chick to adult size and to determine nest fate for late and surviving attempts.

After loggers had been installed I checked on egg stage survival at study nests from vantage points at least 500m away to avoid observer-induced recesses in the nest temperature record. Where this was not possible I waited at least a full incubation term (27 days) from the date that the temperature logger was installed before checking survival. I assumed that nests had failed during incubation if there was no evidence of eggs or chicks at a proven breeding lake and if small egg shell fragments, indicative of hatching, were absent from, or large crushed or punctured egg shell fragments, indicative of predation, were present close to a previously active nest. I assumed attempts had reached the chick-rearing stage if chicks were present or if absent, small egg shell fragments were present in the upper part of the nest material and assumed that a nest was successful if at least one chick was present on a visit that I made to all nests approximately four weeks after hatching. For nests that failed during incubation I estimated the date of failure from a model that used the date when nest and ambient temperature traces converged after a period of incubation (see Chapter 2, section 2.3.2, *Nest temperature models* – ‘convergence of nest and ambient temperature, model).

I used egg flotation, relative chick size measures and nest temperature signatures to supplement observations of clutch increase and hatching to determine timing of breeding. This was required to allow modelling of nest survival rates in program MARK (see Chapter 3, section 3.3.3, *Timing of breeding attempts,* for details of how laying date was determined).

6.3.1 Nest temperature records

In 2008 temperature loggers were primarily used as a replacement for field visits to provide basic nest survival information and as a result the recording interval was set too long to provide useful attendance information. This study therefore uses data from 2006 and 2007 breeding seasons only. Temperature loggers were installed when active nests were located as part of periodic monitoring visits. As a consequence, temperature traces at any given breeding attempt began sometime after the start of incubation and continued until the logger was removed or full, sometime after hatching. In 2006 I used Tinytag® TGP4020 loggers (Gemini Data Loggers UK Ltd) attached to a 2m long 'Flexible Thermister Probe' (PB-5006-1M5) and in 2007 iButton® (Maxim/Dallas Semiconductor Corp., Sunnyvale, CA) DS 1922 L-F5 Thermochron data loggers. The lower cost of these units allowed recording at more nests than was possible in 2006. The average incubation recess recorded during 176 hours of one-minute instantaneous sample observations at 11 breeding sites during an earlier study was 6 minutes (SD = 6.3, *N* = 11, Natural Research unpublished data). I assessed that a recording interval of comparable length would be the best compromise between capturing recess events and ensuring recording throughout the entire incubation period. The 6 minute recording interval allowed recording for 33 days. I set data loggers to start recording on the hour so all records were directly comparable. To install a Tinytag probe I made an incision from the centre of nest to approximately 1m away. I located the end of the probe just above the surface of the nest material in the base of the nest and then fed the probe cable into the incision. The attached logger unit was buried at the end of the incision. Ibuttons were housed at one end of a short plastic tube pushed into the centre of each sample nest until it was flush with the nest base. Before inserting each logger into the tube I covered the uppermost surface with a piece of thin black polyester gauze. Hartman and Oring (2006) found that uncovered 'iButtons' were prone to removal by incubating birds or predators in their study of nest survival in long-billed curlews (*Numenius americanus*). Installation time was approximately five minutes for a Tinytag logger and one minute for an iButton. I observed incubating birds before and after installation of both iButtons and Tinytags and saw no difference between pre- and post- installation behaviour. Loggers were removed after the chicks had left the nest. Before removal I measured the depth of nest material above the monitoring surface of the logger to allow me to test if nest temperature was affected by this.

I imported temperature records for each sample nest into Microsoft *Excel*®. For the analysis I removed the part-day when the logger was installed to minimise the chances of disturbance effects of my nest visit on nest temperature readings and nest attendance behaviour. I terminated temperature records at the end of the last full day before failure or hatching. Pre-hatching nest temperature patterns are readily distinguished from post-hatching records (see Chapter 2, Figure.2.4). I visually inspected each temperature trace to ensure that the predictive models had not overestimated hatching date. Where this occurred (*N* = 3) I estimated hatching using the date predicted by the peak daily maximum nest temperature because this model tended to slightly underestimate hatching date (see Chapter 2).

I identified the start or end of an incubation recess when a temperature record decreased or increased by at least 2°C from the preceding record providing that this change was maintained for a minimum of two 6 minute records (following guidlines in Manlove & Hepp 2000). Compared to an earlier observational study, (see above) the number of recesses identified using these criteria was much lower. A possible reason for this was that the temperature increase per record typical of a bird resuming incubation was smaller than the decrease that occurred when leaving, probably because the bird took a while to settle on the nest and its underside was wet. I compared the difference in the number of decreasing records at the start of the recess with the number of increasing records after a bird had returned to the nest. The ratio between the number of increasing and the number of decreasing records averaged for 20 recesses that satisfied the criteria was 1:1.8 suggesting that temperature took almost twice as long to recover at the end compared with the start of the recess. I therefore relaxed the criteria determining the end of the incubation recess to allow the increase of 2°C to take place over two records. A 2°C decrease in nest temperature occasionally occurred in the middle of a series of smaller decreases, indicating that the recess began before the criteria were satisfied. In these cases I adjusted the recess to start with the first decrease in the series. Conversely if the recorded temperature began increasing before the ‘end of recess’ criteria were satisfied, I ended the recess at the first increasing record in the series (following Hoover *et al.* 2004).

Temperature records that were not identified as part of an incubation recess were averaged to obtain the nest temperature each nest. For each nest I calculated the number and duration of recesses for each day relative to the laying date and for each hour of the day.

To examine differences in nest attendance in relation to nest age I divided recess data into four groups approximately corresponding to the 4-week red-throated diver incubation period (1-7, 8-14, 15-21, 22-27 days) and divided the total number of recesses and total duration of recesses for all sample nests by the number of days with recess information in each weekly group to obtain averages for each week. To describe differences in nest attendance through the day I grouped individual recesses into hourly categories. To describe variation in nest attendance behaviour in relation to egg size I divided sample nests into two groups according to whether egg volume for the nest was below or above the mean value for all nests in the sample (mean: 81cm^3, N = 20). I also examined differences in the number and duration of recesses for nests that failed during either incubation or chick rearing compared with those that successfully raised one chick to at least four weeks.

6.3.2 Statistical Analysis

I used independent t-tests to compare differences in average nest temperature and number and duration of incubation recesses between nests with larger and smaller than average eggs and between failed and successful nests. I tested for a relationship between the number of incubation recesses and the nest age by regressing the number of daily recesses against nest age for each individual nest and then using a one sample t-test to test for differences between the slope coefficients for each nest. I repeated this procedure to test for differences in the number of recess through the day. Statistical tests were carried out using SPSS (SPSS Inc. version 15). Data were checked for normality before carrying out parametric tests, and regression model residuals were also checked. All tests were two-tailed with the significance level set at P = 0.05. For t-tests I checked for significant variance between sample groups using Levene’s test and report the t-test statistics that reflect the results of this test. Means with ± 1 standard error are reported.

I used the nest survival model in program MARK (White & Burnham 1999) (see Chapter 3, section 3.3.4 *Preparing survival data for Program MARK,* for details of data preparation for nest survival modelling using MARK) to evaluate four candidate models based on the predictions I made relating to the effects of nest temperature and the number and duration of recesses on nest survival (Table 6.2). In addition to an intercept only model where survival was held constant for the study period (model 1) I tested individual effects of average nest temperature (model 2) the average number of recesses (model 4) and the average recess duration (model 6). I tested the fit of these models against top models from Chapter 3 (nest age, model 3) and Chapter 4 (laying date + egg volume, model 5). I used Akaike's Information Criterion value corrected for small sample sizes (AIC_c) to rank competing models with the model best supporting the data identified as that with the lowest (AIC_c) value. I used the associated Akaike weight (W_i) to quantify the degree of support between competing models and assumed that there was considerable support for a difference between two models if the Δ AICC values differed by greater than 2.0.

6.4 Results

I retrieved nest temperature records from 20 first breeding attempts for which survival information was also available (18 two-egg clutches and 2 one-egg clutches). The average nest temperature after removing recess records was 23.4 °C ± 0.3 °C ($N = 20$) with the average temperature at individual nests ranging from 20.9 °C to 26 °C (Table 6.1). Average daily nest temperature was higher, although not statistically significant, for nests where temperature loggers had more than 10mm of overlying nest material when removed (24.23 ± 0.53 °C, $N = 6$) compared with loggers that had less than 10mm of overlying nest material (23.03 ± 0.33 °C, $t_{18} = 1.99$, $P = 0.07$). For the sample as a whole the average number of recesses was approximately one per day (1.01 ± 0.07, $N = 278$, range: 0 - 7) and the average duration of recesses was just over 20 minutes (21.7 ± 3, range: 0 – 576). The number and duration of recesses was uncorrelated ($r = 0.25$, $P = 0.29$, $N = 20$). The number of daily recesses was not related to nest age (one sample t-test: $t_{18} = 1.04$, $P = 0.31$) or hours of the day (one sample t-test: $t_{18} = 1.3$, $P = 0.21$) based on difference between individual regression slopes of each nest. Similarly there was no linear trend in the duration of incubation recesses with nest age (one sample t-test: $t_{18} = 0.72$, $P = 0.48$) but a significant relationship between the duration of recesses and hour of the day (one sample t-test: $t_{18} = 2.51$, $P = 0.01$). The number of recesses peaked in the hours around dawn and during the evening hours particularly just before dark with recesses least frequent around noon and during the afternoon hours (Figure 6.1). On average the shortest recesses occurred around noon and during the afternoon and the longest recesses just after dawn and during the evening hours (Figure 6 2).

Nest temperature for nests with above and below average clutch volume was very similar (23.5 ± 0.49 °C, *N* = 10; 23.3, ± 0.37 °C, *N* = 10 respectively). Although the number and duration of recesses was higher for nests with below average clutch volume (0.93 ± 0.20 recesses per day, *N* =10; 27.5 ± 8.1 min, *N* = 10, respectively) than for nests with above-average clutch volume (0.58 ± 0.16 recesses per day, t_{18} = 1.39, *P* = 0.18; 19.3 ± 2.8 min, t_{11}= 0.96, *P* = 0.36 respectively) this was not statistically significant. Nests that failed had very similar nest temperatures to those that raised at least one chick to four weeks (23.1 ± 0.65 °C, *N* = 7; 23.6, ± 0.32 °C, *N* = 13 respectively), and I found no significant differences between the average number of recesses and the number of nests that failed (0.9 ± 0.21, *N* = 7) compared with those that were successful (1.0, ± 0.22, t_{18} = 0.58 =*P* = 0 57). Similarly there were no significant differences between average recess duration for nests that failed (24.3 ± 11.21 min, *N* = 7) compared with those that were successful (21.8, ± 2.46 min, t_6 = 0.21, *P* = 0 84).

The model where nest survival was held constant (model 1) was the best supported model in the MARK analysis (Table 6.2). Models with an effect of nest temperature (model 2), and average number of recesses (model 4) had ΔAIC_c values of less than 2 but the 95% confidence interval for the beta estimates in both models overlapped zero suggesting little variation in survival with nest temperature and the number of recesses. Models with an individual linear effect of nest age (model 3) and additive effects of laying date and egg volume (model 5) were also supported within this candidate set but as with models 2 and 3, the beta estimates suggested little variation in related nest survival rate.

Table 6.1 Average daily nest temperature and recess information for 20 red-throated diver nests.

Sample nest	Number of sample days	Nest age: range of days in sample	Average incubation temperature(˚C)	±1SE	Average number of recesses	±1SE	Average duration of recess (mins)	±1SE
1	20	3-22	22.6	0.03	3.0	0.43	13.8	0.53
2	20	4-23	23.8	0.02	1.1	0.25	17.1	1.62
3	19	7-25	26.0	0.02	0.6	0.19	16.9	1.58
4	14	14-27	23.2	0.02	0.3	0.13	12.0	0.00
5	18	10-27	23.1	0.03	1.2	0.26	14.7	0.86
6	18	10-27	22.4	0.04	0.6	0.18	19.2	3.56
7	6	20-25	25.5	0.05	0.2	0.17	18.0	0.00
8	3	2-4	21.3	0.06	0.0	0.00	0.0	0.00
9	5	23-27	23.7	0.07	1.8	0.58	92.0	38.39
10	19	8-26	21.5	0.03	1.2	0.24	21.5	3.88
11	9	19-27	24.1	0.06	1.4	0.38	27.7	6.36
12	20	4-23	25.1	0.02	1.7	0.27	12.2	0.24
13	5	21-25	22.5	0.05	0.8	0.37	15.0	3.00
14	7	21-27	23.3	0.06	1.6	0.78	22.9	3.60
15	24	4-27	24.5	0.03	0.6	0.16	19.3	2.83
16	23	5-27	23.8	0.02	0.8	0.22	25.3	5.35
17	12	2-13	20.9	0.03	0.8	0.35	14.0	2.00
18	13	15-27	22.8	0.04	0.1	0.08	36.0	0.00
19	4	9-12	23.5	0.08	1.0	0.41	15.0	3.00
20	20	8-27	24.3	0.02	1.1	0.20	40.9	26.19

Table 6.2 Model selection results for the effects of nest temperature and attendance behaviour on red-throated diver nest survival, compared with the best supported model from the variation through the breeding cycle analysis (Chapter 3, nest age model) and best supported model from the effects of date and individual quality nest survival analysis (Chapter 4, laying date + egg volume model), Mainland Shetland, Scotland, 2006-8. AIC_C = Akaike's Information Criterion (corrected for small sample size). Models are ranked in ascending order of $\Delta AIC_{c;}$ values. The intercept model assumes constant survival.

Model No.	Model	Deviance	Parameters	AIC_c	Δ AIC_c	AIC_c Weight (w_i)
1	Intercept	46.87	1	48.87	0.00	0.27
2	Nest temperature	45.36	2	49.38	0.51	0.21
3	Nest age	46.12	2	50.14	1.27	0.14
4	Recess number	46.18	2	50.20	1.32	0.14
5	Laying date + egg volume	44.30	3	50.33	1.46	0.13
6	Recess duration	46.87	2	50.88	2.01	0.10

Figure 6.1 Number of incubation recesses through the day for red-throated diver, Mainland Shetland, Scotland, 2006-2007.

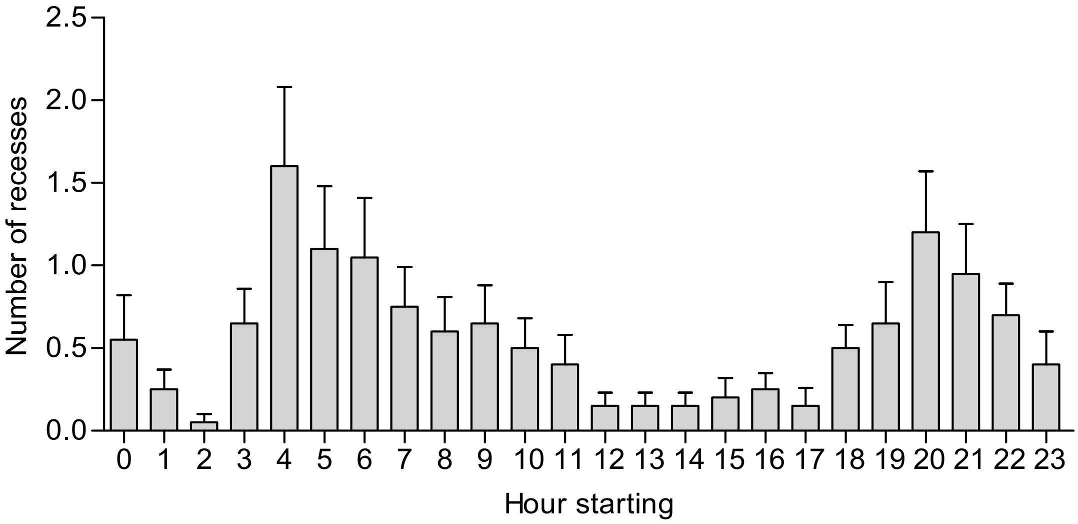
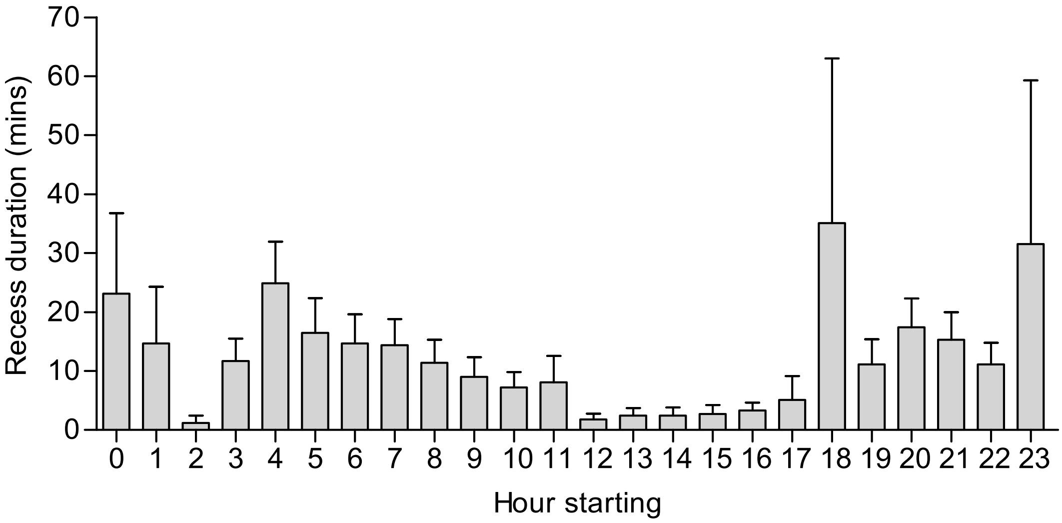


Figure 6.2 Duration of incubation recesses through the day for red-throated diver, Mainland Shetland, Scotland, 2006-2007.



6.5 Discussion

Although average daily nest temperature was well below typical avian egg temperature of 30 - 40 °C (Webb 1987), the average standard error for sample nests was ± 0.3°C indicating that temperature varied little when the incubating adult was on the nest. This constancy of temperature is typical of egg temperature regimes in species that regulate incubation temperature closely (e.g. Afton 1979; Morton & Pereyra 1985). Thus temperature data loggers installed in the base of nests appear to be a good relative measure of incubation temperature.

As incubation progressed some temperature loggers became covered with new or displaced nest material. These loggers recorded a higher average nest temperature compared with exposed loggers indicating that they were insulated from cooler temperatures recorded at the surface of the nest bowl and suggesting that nest temperature may have been directly affected by environmental conditions. It is plausible that comfort movements of incubating birds allowed the nest bowl to be exposed to brief but frequent environmental cooling effects particularly of the wind (see Poussart *et al.* 2000), depressing temperatures of the more exposed loggers, and consequently also of the eggs, that were similarly exposed to these cooling effects. The extent to which the influence of environmental conditions vary with nest structure, adult body mass and condition and how this might affect embryo development and subsequent chick survival was not examined but merits further research.

The recess criteria identified on average one recess per day, suggesting that incubation was almost continuous. In an earlier study of 11 pairs and comprising 176 daylight hours of one-minute instantaneous behavioural sampling, the average number of recesses was 3.9, corresponding to 4.3 recesses per 18 hours of daylight monitoring (Natural Research, unpublished data) which is greater than I detected here. Setting the recording interval too long — sixty percent of the recesses in the above study had durations of less than six minutes — or overly restrictive recess criteria are two possible reasons for this disparity. Alternatively, real differences between individual study birds or between studies may explain these differences. The 6 minute recording resolution and recess criteria did detect patterns in the number and duration of recesses with nest age and through the day suggesting that they were broadly appropriate for detecting variation in incubation behaviour. Red-throated divers breed in cool climates where the rate of heat loss from the nest can significantly affect breeding success (Reid *et al.* 1999). This may be particularly relevant for divers because they access nests directly from the water and this may slow down reheating of the eggs after each recess due to the cooling effect of water transferred from the underside of the adult and might suggest a selection pressure for an incubation regime that minimises exposure of the eggs and the number of nest changeovers. This, to some extent may explain the constancy of red-throated diver incubation.

The length of individual recesses varied substantially probably reflecting different reasons for the recess. Shorter recesses lasting up to *ca.* 20 minutes often take place to allow pair-bond strengthening behaviour after the return of an off-duty bird or in response to intruders on the breeding lake (Cramp & Simmons 1977, S. Hulka pers. obs.). Interestingly, some of the longest recesses occurred during the hours of darkness. Red-throated divers are visual foragers (Ashmole 1971) and so these recesses are unlikely to represent foraging periods. Otters (*Lutra lutra*) are the main mammalian predator in this area, are largely nocturnal (de Leaniz *et al.* 2006) and present risks to both the breeding attempt and adult birds. It is therefore probable that some of these longer recesses occurred when otters were in the vicinity of the nest.

Models based on optimal parental investment predict an increase in nest defence as incubation progresses due to increasing investment by adults in the breeding attempt and the diminishing possibility of re-nesting (Knight & Temple 1986; Montgomerie & Weatherhead 1988; Redondo 1989; Westneat 1989; Brunton 1990). Although there was no linear trend in the number of recesses compared to nest age, the number of recesses peaked during the second week of incubation and then followed a decreasing trend to a minimum in the week before hatching and suggests that increasing parental investment may be a characteristic of red-throated diver incubation behaviour. Individual birds incubate continuously for long periods often in exposed locations surrounded by potential nest predators necessitating constant vigilance. Assuming these demands make incubation energetically costly, it seems likely that birds would seek to maximise their increasing investment in the breeding attempt by increasing parental investment as incubation progresses.

During daylight hours, eggs were left unattended most frequently and for longest during the early morning and late evening, with only occasional short absences during the mid day and afternoon hours. Results from Chapter 5 found that nests closer to the water edge had improved survival chances suggesting that predation risk was related to activity levels around the nest (see Conway & Martin 2000; Ghalambor & Martin 2002) rather than the length of time eggs were left exposed. Concentrating incubation recesses during periods of low light may be an effective way of minimising the chances of predators detecting nests. It is also plausible that the cryptic qualities of eggs are enhanced at low light levels. Future experimental research to test the effects of light levels on nest detection probabilities may help explain red-throated diver incubation rhythms. Conversely, the low incidence of recesses during the midday and afternoon may have evolved to minimise nest detection by limiting movement in the vicinity of the nest. In addition, because incubation costs may be especially high for species nesting in cold environments (e.g. Cresswell *et al.* 2004), nest attendance during the warmest part of the day is likely to have minimal energetic demands on adults and this may allow egg temperature to be maintained closer to the optimum for embryo development (Ardia *et al.* 2009). Another possibility is that high nest constancy during this period resulted from a need to protect eggs from the damaging effects of high temperatures; however Webb (1987) has suggested that eggs of most species can tolerate temperatures of *ca.* 40°C for several hours. Daily ambient temperature peaks were always well below 40 °C in this study and it therefore seem unlikely that high ambient temperature constrained the number of incubation recesses in the middle of the day.

There was a weak trend for birds with larger than average clutch volumes to take fewer and shorter recesses. Although not significant, the sample size was small. This finding is in keeping with other studies that have found a positive relationship between nest attentiveness and individual quality (Ardia & Clotfelter 2007; Ardia *et al.* 2009) and may suggest that higher quality birds had greater energy reserves which allowed them to minimise foraging and maximise nest attentiveness.

Nest temperature and nest attentiveness was not related to breeding outcome. For a species where incubation can be almost continuous the effect of differences in nest temperature and nest attendance on breeding outcome may be subtle and only be detectable with larger samples or in longer term studies, during years of unusually high predator pressure or particularly poor climatic or foraging conditions. Alternatively their effects might not reduce nest survival but might have repercussions for chick condition and survival after fledging.

In the MARK analysis, models with an effect of nest temperature and average number of daily recesses received less support than the model where survival was held constant. Although this agrees with a lack of relationship between these factors and breeding outcome, the fact that the two best models from earlier analyses in this study; nest age [Chapter 3] and laying date + egg volume (Chapter 4) were also indistinguishable from the constant survival model, suggests that the small sample size was affecting the credibility of this result and larger sample sizes are required to fully assess the effects of nest temperature and recess activity on nest survival.

Red-throated divers appear to optimise their energy resources for current and future reproductive attempts principally by employing diurnal activity patterns and behaviours that minimise the chance of predators detecting nests. Although there was evidence to suggest that parental investment may have increased with nest age, extended night time recesses were probably a response to predators and may suggest that protecting the current breeding attempt is relatively unimportant compared with ensuring parental survival. This may be expected of a long-lived species such as the red-throated diver, where continued adult survival to breed in future years is likely to be more important than the outcome of the current breeding season. Recent studies have highlighted substantial energetic costs associated with maintaining egg temperature during incubation (Reid *et al.* 2000), particularly in cold climates (Creswell *et al.* 2004). The impact of these costs on chick quality; resource allocation to the chick-rearing stage within the same breeding attempt, subsequent breeding attempts and breeding success are unclear. Given the harsh climatic conditions and exposed locations characteristic of red-throated diver nest sites, determining the importance of these costs is likely to be important for understanding of the mechanisms that underlie population dynamics in the species.

7 General discussion

The marine environment is extensive, diverse and heterogeneous and as a consequence represents a vast food, energy and raw materials resource. Some of these resources have already been exploited and the process has exerted considerable pressure on populations within marine ecosystems. Others, in particular renewable energy, remain largely untapped, but are likely to play a major role in fulfilling global energy demand in the future (Pelc & Fujita 2002), and as a result add to the range of existing pressures. Despite the importance of the marine environment we know very little about many marine species and only relatively small areas are protected. In order to protect and conserve its biodiversity we need to understand the breeding biology of the inhabitants. Seabirds are found in all marine habitats; distributed worldwide and are important because they can be used as indicators of the health of the wider marine ecosystem (Montevecchi & Myers 1995; Parsons *et al*. 2008). Despite this, important research needs conducting on nearly every group of seabirds, in all aspects of their lives (Schreiber & Burger 2002). Population changes are often an important indicator of changes in the marine environment and these changes result from the dynamic balance between birth and immigration, and death and emigration. Understanding population change requires an understanding of both these effects. In this study I focused on the effects relating to birth. Specifically, I investigated the factors that determined breeding success in a top-level seabird predator — the red-throated diver, a species with demonstrated vulnerabilities to human disturbance (Pakarinen & Järvinen 1984), marine ecosystem changes (Eriksson & Sundberg 1991; Ball 1994), and a predicted vulnerability to climate change (Huntley *et al*. 2006). To achieve this I primarily used nest survival modelling (White & Burnham 1999). Nest survival is an important metric for assessing population change and is a key tool which has undergone important recent developments allowing the effect of environmental and behavioural factors on nest survival to be tested (Jehle *et al*. 2004).

Briefly, the analyses from this study population indicate:

- The widely used Mayfield Method (Mayfield 1975) is a relatively uninformative model for assessing nest survival rate in red-throated divers because nest survival in this species is affected by time-specific, biological and environmental factors (Chapters 3, 4 and 5)

- Red-throated diver nest survival; increases incrementally with nest age (Chapter 3); decreases with advancing laying date for all study pairs but is most pronounced for lower quality pairs (Chapter 4); decreases with nest distance from the shore but increases with increasing daily wind speed and rainfall (Chapter 5); decreases as the proportion of time that wind direction corresponded with the longest axis of the lake increases, particularly for lakes at lower elevations (Chapter 5).

- No detectable effect on nest survival, of year, breeding stage, lake size, island nests, and distance to nearest road (Chapters 3 and 5)

- First breeding attempts have significantly higher survival rates than second attempts, but have similar mean clutch egg volumes (Chapter 3 and 4)

- Two egg clutches have significantly larger eggs than one-egg clutches (Chapter 4)

- A clear pattern to diurnal nest attendance with the majority of recesses occurring away from the middle part of the day (Chapter 6)

Taken together, these findings suggest that predation risk is likely to be a key factor determining red-throated diver breeding performance, with breeding pairs more successful when predation risk is low, or if they are able to minimise the risk because they have the nutritional resources or nest site quality that enable them to do this. Earlier studies have suggested that environmental effects may be important in determining red-throated diver breeding performance. For example, Dahlén and Eriksson (2002) found warmer drier improved breeding performance. I found that adverse weather conditions improved survival, most likely because avian predators in particular were less active, but presumably also because there was little negative effect of adverse weather on adults or the survival of eggs or chicks. The minimal direct effect of adverse weather on red-throated diver nest survival is unsurprising as core breeding areas are in the high arctic where conditions should exert a strong selection pressure for characteristics that counteract the negative survival effects of adverse conditions. If predation risk has a strong influence on determining survival then the density, distribution, prey priorities and foraging behaviour of red-throated diver egg and chick predators will to some extent determine breeding success. Moreover, findings from this study suggest that that individual quality, of adults and/or breeding sites plays an role in offsetting predator risk.

In addition to indicating the importance of these aspects of red-throated diver breeding biology to breeding performance, the results have highlighted further research and monitoring that is desirable if we are to more fully understand the mechanisms underlying red-throated diver reproductive performance and hence effectively monitor and provide management options to conserve population health. We know very little about the factors that influence individual quality in marine foraging areas. Adult nutritional quality is affected by the composition and availability of fish prey on wintering grounds and along migration routes and in coastal foraging areas during the breeding season. Identifying these areas and routes, and assessing prey composition for individually identifiable birds with known breeding locations will allow the effects on nest survival of factors relevant to marine foraging areas to be incorporated into models, and their relative importance tested alongside environmental, biological and behavioural factors identified in this study. Studying seabird behaviour at sea is a challenging area of research (Schreiber & Burger 2002). However recent developments in global positioning system (GPS) loggers and satellite tracking technologies for use with seabirds, have resulted in miniature devices that are able to provide detailed positional data over extended periods (e.g. Guilford *et al.* 2008; Kotzerka *et al.* 2010; Votier *et al.* 2010). This technology could provide data to help address questions relating to the effects of foraging location, and prey type and availability on breeding performance, and their use for this type of research with red-throated divers during the breeding and non-breeding periods should be evaluated. Additionally data from these technologies can provide valuable behavioural information relevant to assessing the effect of offshore renewable developments on red-throated divers.

Quality may be the phenotypic quality or body condition of breeding individuals or the quality of their breeding environment, in particular the quality of breeding sites and territories (Verhulst & Nilsson 2008). Red-throated divers are restricted in the range of breeding sites they use. In this study, all bred singularly on lakes, the majority of which were shallow isolated water bodies less than 1 hectare. This resource is limited and also vulnerable because smaller pools in particular are susceptible to drying out or sudden drainage resulting from adjacent peat erosion (S.Hulka, D.B Jackson pers.obs.). Thus each lake is relatively important for maintaining breeding population levels. Determining the number and location of all potential breeding lakes for a population; long-term lake habitat monitoring, in particular of erosion adjacent to breeding lakes and lake water levels; and developing a quality index for each lake, perhaps based on average long-term breeding output (Natural Research, unpubl. data) should be important components of red-throated diver conservation planning, ensuring that changes in lake habitat quality are identified early.

One aspect of breeding lake quality that may be relatively independent of biotic lake characteristics is predator pressure in the immediate vicinity of the lake, however given the importance of predation risk to nest survival found in this study, future research should distinguish the relative importance to nest survival of potential predators and population and activity monitoring data for key predator species obtained to assess the effect of these predators on breeding performance. Because nests are in open locations and lakes are usually small, camera monitoring of nest sites and breeding lakes is likely to be effective in identifying both egg and chick predators.

My research findings have some limitations and some areas where analysis could be improved. The study sample was taken from a single core UK breeding area on Mainland island Shetland, and although originally intended, it was not feasible to study a second geographically different sample. Had this been possible it would have allowed me to compare results from the two populations and better assess the relevance of results to the wider UK breeding population. Future research should therefore be conducted on red-throated diver populations elsewhere in the UK to allow for this. On a larger geographical scale, the study population is not representative of overall global red-throated diver population which predominantly breeds in the high arctic where conditions are more severe and the breeding period is constrained by the date of spring thaw and autumn freezing of breeding lakes. In these areas it is possible that poor weather conditions do have a negative effect on nest survival unlike the findings here. Nonetheless current findings and future research from this study area, located as it is at the southern edge of the red-throated diver breeding range, are important because recent climate models predict that this breeding range boundary will recede north-westwards resulting in the species no longer breeding in the UK by 2100 (Huntley *et al*. 2006). Monitoring likely indicators of the effects of climate change such as breeding performance, egg size and changes in occupancy (Crick 2004) will provide useful information about how the species is responding to climate change. Moreover modelling the effect of environmental covariates indicative of climate change such as sea surface temperatures would provide additional evidence about the effect of climate on the species.

In the nest survival modelling analysis used in Chapters 3-6 the top model is the one that best explains the variation in the data, and the analysis follows the rule-of-thumb convention that top rated models with differences in ΔAIC_C value of less than 2.0 have approximately equal weight and are supported by the data (Cooch & White 2005). To determine which is the best model from a set of supported models requires a measure of the degree of uncertainty to be incorporated. This is achieved using model averaging. I was not confident of correctly applying model averaging for some of the nest survival models that I had constructed, and therefore did not report model averaged results. In future analyses model averaging should be incorporated. Additionally, some parallel analysis of the nest survival datasets, for example using generalised additive models (GAMs) (Hastie & Tibshirani 1990) or generalised linear models (GLM) (Nelder & Wedderburn 1972), would be useful to evaluate the validity results from the MARK analysis.

The usefulness of the information-theoretic modelling approach is determined by the biological relevance of hypotheses that models are based on. Developing good hypotheses and wisely evaluating the results of modelling analysis is benefited by a detailed knowledge of the species in the field situation where the data has been collected and acquiring this knowledge should be encouraged as it will increase the value of research findings.

To provide timing of breeding and failure information for nest survival analyses I used temperature records from data loggers installed in the base of nests. This technique proved to have no significant impact on breeding success; allowed fewer visits to breeding sites; more nests to be included in nest survival analysis; nests without eggs to be remotely monitored for evidence of subsequent incubation, and greatly improved the accuracy of timing of failure compared with periodic nest visits. These relatively cheap devices should be considered an essential tool for future red-throated diver occupancy and nest survival monitoring.

In this research I have identified and distinguished the relative importance of some of the factors affecting red-throated diver breeding performance. Based on these findings I have suggested areas of additional research and monitoring that should improve our understanding and allow informed conservation priorities for the species to be set. Red-throated divers breeding in this area face potential threats from on- and offshore renewable energy developments and from the effects of climate change. Their likely responses to such complex changes in their breeding environment are unclear and difficult to predict. Under these circumstances a detailed understanding of red-throated diver breeding biology, and the factors determining occupancy of breeding sites and productivity, should optimise the probability of identifying problems at an early stage and facilitate informed conservation planning to address issues before they have detrimental effects on population health.

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