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Reproduction of Coastal Birds Breeding in the Wadden Sea: Variation, Influencing Factors and Monitoring

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Stefan Thyen

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Wilhelmshaven

Gutachter: Prof. Dr. Peter H. Becker

Zweitgutachter: Prof. Dr. Franz Bairlein

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Summary

Among coastal birds breeding abundantly in the Wadden Sea, there are several species characterised by striking population trends during the second half of the 20th century, for example exponential increases in breeding populations of some gull species. High abundance and positive or stable population trends suggest *a priori* a high attractiveness and a high reproductivity of Wadden Sea breeding habitats. However, this assumption has hardly been studied, in particular in common species such as the Black-headed Gull *Larus ridibundus* and the Redshank *Tringa totanus*. The present study, therefore, focussed on the hypotheses that most coastal bird species breeding in the Wadden Sea are highly productive and that relatively well known population trends are largely explainable by annual reproductive output. Besides determining and assessing hatching and breeding success, the study was aimed at identifying effects of selected influencing factors (weather: Black-headed Gull; habitat and nest site selection: Redshank) on breeding performance (variability in life-history traits, hatching and breeding success). Reproductive traits and their variability were additionally intended to be assessed as indicators within a program on monitoring breeding success of coastal birds. Common Terns *Sterna hirundo*, Herring Gulls *Larus argentatus*, Black-headed Gulls, Oystercatchers *Haematopus ostralegus*, Avocets *Recurvirostra avosetta* and Redshanks representing a wide range of different life-history strategies and ecologies were studied during the mid 1990s and during 2000/2001 (Redshank). Altogether, 17 breeding sites on islands and the mainland coast were studied throughout the German part of the European Wadden Sea.

A distinct spatiotemporal variability was found in chick development and/or annual hatching and breeding success during 1996 and 1997 with the exception of Herring Gulls, which presumably used garbage dumps as consistent food supply. This was due to short-term and small scale occurrence of predators and flooding. Overall, breeding performance was mostly more favourable on islands and in 1997 compared to 1996, which was attributed to fewer mammalian predators on islands and a relative shortage of benthic food due to a severe winter preceding the 1996 breeding season, respectively. Average annual reproductive output was assessed to be concordant with population development in Common Terns (0.6 fledglings * pair^{-1} / population decreasing), Black-headed Gulls (1.0 / increasing) and Oystercatchers (hatching success up to 97 % / increasing). Reproduction of Herring Gulls was by far higher than that needed to explain the current equilibrium population (0.8-1.5 fledglings * pair^{-1}), but those of Avocets (0.1 fledglings * pair^{-1}) and Redshanks (hatching success not exceeding about 30%) were considerably lower. Causes of these inconsistencies including the lack of reliable demographic data and migratory processes within the ecosystem are discussed.

Weather parameters as well as habitat and nest-site supply both were identified as considerable parameters affecting coastal bird reproduction. It was shown for Black-headed Gulls that rain and temperature during different phases of breeding performance advance hatching and breeding success, presumably by enhancing time allocation (nest and brood attendance) and particularly terrestrial food availability. Although a negative effect of rain on survival of neonates was found to be similar to the results of most comparable studies in coastal birds, the results suggest that supplemental usage of terrestrial food may be responsible for a relatively constant high reproductive output even in the long-term. As found in Redshanks, hatching success of saltmarsh breeding birds concealing their clutch in vegetation is dependent on phenological and successional status of the habitat vegetation. It was shown that early breeding favours successful incubation presumably by temporally avoiding high predation pressure. Early breeding itself was facilitated by supply of well structured and well concealed nest-sites in plant communities of advanced chronosequence available already early in the season. In contrast to open-nesting species such as Oystercatchers, Redshanks should benefit from breeding away from the shoreline and tidal flat foraging territories owing to nest-site quality increasing with ground elevation, chronosequence and distance to shoreline, respectively.

The results obtained by the studies comprising this thesis have several implications for monitoring the breeding success of coastal birds. They suggest that it is well feasible to record annual hatching and breeding success of several species at several breeding sites. Data appear well suited to explain, to model and to predict population growth rates provided that further important demographic data on subadult and adult mortality of the population in question are available. Those data are completely lacking, for example, in Black-headed Gulls and Redshanks, and should be recorded within integrated population monitoring. The results presented in this study furthermore suggest that life-history traits (clutch size, chick development) as well as hatching and breeding success are parameters sensitive to a variety of environmental factors. It is consequently urgently recommended to include and implement the parameter of breeding success within the Trilateral Monitoring and Assessment Program of the Trilateral Wadden Sea Co-operation to meet the respective ecological targets.

Zusammenfassung

Viele Küstenvogelarten brüten mit relativ hohen Dichten und mit teilweise bemerkenswerten Populationsentwicklungen während der zweiten Hälfte des 20. Jahrhunderts im Bereich des Wattenmeeres. Beispielhaft genannt seien die exponentiellen Bestandsentwicklungen einiger Möwenarten. Die hohen Brutdichten und positive bzw. stabile Populationstrends legen *a priori* den Schluss nahe, dass das Wattenmeer nicht nur hochattraktiv für viele Arten ist, sondern auch von hoher reproduktionsbiologischer Qualität. Allerdings wurde diese Annahme bisher an sehr wenigen Arten untersucht, nicht jedoch an sehr häufigen Arten wie der Lachmöwe *Larus ridibundus* und dem Rotschenkel *Tringa totanus*. Die Hypothese der vorliegenden Untersuchung war deshalb, dass die meisten Küstenvogelarten mit einer hohen Reproduktivität im Wattenmeer brüten und dass die relativ gut bekannten Populationsentwicklungen der letzten Jahrzehnte weitgehend durch den jährlichen Bruterfolg einer Art erklärbar sind. Neben Bestimmung und Beurteilung des jährlichen Schlupf- und Bruterfolges war es ein weiteres Ziel der vorliegenden Arbeit, Effekte ausgewählter potentieller Einflussgrößen wie dem Wetter (untersucht an Lachmöwen) und der Habitat- und Nistplatzwahl (Rotschenkel) auf Gelegegröße, Kükenentwicklung, Schlupf- und Bruterfolg zu untersuchen. Darüber hinaus sollte die Eignung dieser wesentlichen reproduktiven Merkmale als Indikatoren für Umweltveränderungen innerhalb eines Monitoringprojektes beurteilt werden. Untersucht wurden Flussseeschwalben *Sterna hirundo*, Silbermöwen *Larus argentatus*, Lachmöwen, Austernfischer *Haematopus ostralegus*, Säbelschnäbler *Recurvirostra avosetta* und Rotschenkel als repräsentative Arten verschiedener Lebenszyklen und Lebensweisen. Mitte der 1990er Jahre sowie in den Jahren 2000 und 2001 (nur Rotschenkel) wurden insgesamt 17 Brutgebiete auf Inseln und am Festland innerhalb des deutschen Teils des internationalen Wattenmeeres untersucht.

Mit Ausnahme der Silbermöwe wurde in den Jahren 1996 und 1997 eine ausgeprägte räumlich-zeitliche Variabilität in den Parametern der Kükenentwicklung bzw. im jährlichen Schlupf- und Bruterfolg ermittelt. Die Ursache dafür waren kurzfristig und kleinräumig auftretende Überflutungen und hohe Prädation. Generell brüteten die Vögel auf Inseln erfolgreicher als am Festland, was auf eine relativ geringe Dichte von Kleinsäugern auf den Inseln zurückgeführt wird. Ebenso waren die Vögel im Jahre 1997 erfolgreicher als im Jahre 1996, wofür der Eiswinter 1995/96 und die daraus resultierende geringe Verfügbarkeit benthischer Nahrung verantwortlich gemacht wird. Die mittleren jährlichen Bruterfolge der Arten Flussseeschwalbe (0,6 flügge Küken * Paar^{-1} / abnehmende Bestandsentwicklung), Lachmöwe (1,0 / zunehmend) und Austernfischer (Schlupferfolg bis zu 97% / zunehmend) waren konsistent mit deren Bestandsentwicklungen der letzten Jahre. Der Bruterfolg der Silbermöwe (0,8 – 1,5 Jungvögel * Paar^{-1}) war deutlich höher als der zur Erklärung des derzeit stabilen Bestandes notwendige. Die Reproduktion von Säbelschnäbler (0,1 Jungvögel * Paar^{-1}) und Rotschenkel (Schlupferfolg höchstens 30%) war dagegen nicht ausreichend, um deren derzeit stabilen Bestände zu erklären. Diese Divergenzen werden teilweise auf das Fehlen ausreichend genauer demographischer Daten zurückgeführt, könnten aber auch ökologische Ursachen wie etwa Migrationsprozesse innerhalb des Wattenmeeres haben.

Sowohl verschiedene Wetterparameter als auch das Angebot an Habitaten und Nistplätzen wurden als bedeutende Einflussgrößen der Reproduktion von Küstenvögeln qualifiziert. Schlupf- und Bruterfolg der Lachmöwe standen in positivem Zusammenhang mit Temperatur und Regen während verschiedener Phasen des Brutgeschäftes. Dieser Zusammenhang ist mutmaßlich auf eine Verschiebung des Zeitbudgets der Elterntiere zugunsten einer verstärkten Brutpflege sowie eine

Verbesserung der Verfügbarkeit insbesondere terrestrischer Nahrung zurückzuführen. Ähnlich vergleichbaren Untersuchungen an Küstenvögeln, wurden aber auch negative Effekte von Regen auf das Überleben frisch geschlüpfter Küken gefunden. Die Ergebnisse legen letztlich auch den Schluss nahe, dass die ergänzende Nutzung terrestrischer Nahrung möglicherweise für einen langfristig konstanten und relativ hohen Bruterfolg verantwortlich sein könnte. Die Untersuchungen am Rotschenkel zeigten, dass der Schlupferfolg von zur versteckten Brut auf Vegetation angewiesene Brutvögel der Salzrasen vom phänologischen und sukzessiven Entwicklungszustand des Habitates abhängig ist. Eine frühe Brut begünstigte eine erfolgreiche Bebrütung, vermutlich durch eine zeitliche Vermeidung eines mit dem Saisonverlauf ansteigenden Prädationsdruckes. Eine frühe Brut wurde ihrerseits insbesondere an reich strukturierten und gut versteckten Nistplätzen in Vegetationstypen fortgeschrittener Zonen der Chronosequenz ermöglicht. Aus diesem Grunde dürften Rotschenkel und andere Arten vergleichbarer Nistökologie davon profitieren, relativ entfernt von potentiellen Nahrungsflächen im Watt zu brüten. Die Qualität potentieller Nistplätze dürfte mit der Bodenerhöhung, der Chronosequenz und der Entfernung zum Watt zunehmen. Habitat- und Nistplatzwahl sowie deren Konsequenzen für die Reproduktion des Rotschenkels unterscheiden sich damit wesentlich von denen offen brütender Arten wie beispielsweise dem Austernfischer.

Die oben erläuterten Ergebnisse erlauben verschiedene Schlussfolgerungen für ein Bruterfolgsmonitoring mit Küstenvögeln im Wattenmeer. Die Untersuchungen haben gezeigt, dass eine zuverlässige Erhebung und Auswertung des Schlupf- und Bruterfolges verschiedener Arten und in verschiedenen Brutgebieten durchführbar ist. Entsprechende Daten sind dazu geeignet, Populationsentwicklungen zu erklären, zu modellieren und vorherzusagen. Voraussetzung dafür ist allerdings, dass weitere demographische Daten der in Frage stehenden Population verfügbar sind, d.h. hauptsächlich zur Mortalität subadulter und adulter Vögel der Population. Entsprechende Daten fehlen für die meisten Küstenvogelarten des Wattenmeeres vollständig, wie etwa für Lachmöwe und Rotschenkel, und sollten im Rahmen eines integrierten Populationsmonitorings dringend erhoben werden. Die vorliegenden Ergebnisse zeigen darüber hinaus, dass reproduktionsbiologische Merkmale wie die Gelegegröße und Parameter der Kükenentwicklung sowie Schlupf- und Bruterfolg sensible Indikatoren verschiedener Umwelteinflüsse und –veränderungen darstellen. Daraus leitet sich die dringende Empfehlung ab, den Parameter „Bruterfolg“ innerhalb des Trilateral Monitoring and Assessment Program der trilateralen Wattenmeer-Kooperation entsprechend der festgeschriebenen „Ecotargets“ umzusetzen.

1. Introduction and Synopsis

1.1. Position of breeding success within avian life-histories

Life-histories of organisms are characterised by specific patterns of diversely developed life-history traits contributing to an optimal fitness by a complex interplay. Major traits in birds include age at maturity, reproductive lifespan, annual adult survival, number of offspring, developmental mode and reproductive effort, which may result in costs of reproduction with its major components clutch and egg size, incubation schedule, parental care (Stearns 1992, Bennett & Owens 2002). These traits are linked by a multiplicity of cost-benefit trade-offs from which those related to current reproduction vs. survival, future reproduction and condition may be the most important: Life-history theory predicts a specific balance of resource allocation to current reproductive value vs. residual reproductive value or, in other words, between reproductive and somatic investments (e.g., Stearns 1992, Glazier 1999, Ricklefs 2000, Bennett & Owens 2002, Martin 2004). Owing to a positive relationship between adult mortality and annual reproductive rate (e.g., clutch size) and a reverse covariation between adult mortality and age at maturity found over a wide range of species, the diversity of “life-history strategies” is distributed on a “slow-fast axis” (Ricklefs 2000, Martin 2004). This axis distinguishes species with high adult survival, late maturity and small clutch sizes (formerly known as “K-strategists”) (e.g., Pianka 1970, but see discussion in Stearns 1992) from “fast” species (“r-strategists” as, for example, songbirds of temperate regions) characterised by low survival, early maturity and large clutches. Life-histories of birds are furthermore characterised by various developmental modes distributed on another continuum: Chicks of altricial species hatch at a relatively early stage of ontogenesis and are dependent on parental brooding and food provisioning within the nest until fledging. Those of precocial species are widely independent, leave the nest soon after hatching and are usually not fed by the parents (Starck & Ricklefs 1998). There are many intermediate modes between these two ends of the continuum.

Organisms have evolved these strategies to maximise fitness, i.e. to maximise the contribution of own genes to future generations relative to the conspecifics within a population (Stearns 1992, Schaefer 2003). In recent years, the value of “lifetime reproductive success” (LRS) has been introduced as a relatively good estimator of fitness (Clutton-Brock 1988, Newton 1989, Barrowclough & Rockwell 1993, Maccoll & Hatchwell 2004). LRS is defined as the number of fledged young that is produced by an individual during its lifespan. Major components of LRS are the number of reproductive events and the breeding success per event which an individual achieved during its life. Breeding success is consequently of fundamental importance in life-histories of birds, although its relative significance depends on the bird´s life-history strategy; it should be less significant for the fitness of a long-lived species, which has the potential to perform many breeding attempts in its lifetime, compared to a short-lived species. Accordingly, life-history theory predicts that long-lived species should value their own life over that of their offspring to optimise fitness by increasing the probability of performing further breeding attempts (e.g., Erikstad *et al.* 1998, Ghalambor & Martin 2002, Mills *et al.* 2005).

The elucidation of life-history concept and the position of breeding success within that concept given above is somewhat abstract disregarding that birds mostly live in groups with competing conspecifics and in an environment with several influencing factors. From an evolutionary perspective, natural selection is assumed to act through these factors on different life-history traits and drive evolution of avian life-histories. Whilst theory on development of life-history traits is widely acknowledged, i.e., balancing resources among traits in a specific manner, there are many different theories on which main selective agents may drive evolution and which may be the key traits upon which natural selection acts (see reviews in, e.g., Ricklefs 2000, Bennett & Owens 2002, Martin 2004). Theories range from food limitation as selective factor acting on clutch size (Lack 1968), parental provisioning ability and developmental mode acting on reproductive rate (Starck & Ricklefs 1998), nest-site and nest predation acting on breeding period (Martin 1995, Bennett & Owens 2002) and parental care (Ghalambor & Martin 2002), climate and migratory behaviour acting on adult mortality (Ghalambor & Martin 2001, Martin 2004) to population density potentially acting on various reproductive traits (Ricklefs 2000). All of these theories are supported by abundant empirical data making it difficult to assess the explanatory significance of each single theory.

However, from an ecological perspective and considering that natural selection acts at the individual level, these insights into evolutionary theory of avian life-histories explain a considerable amount of the theoretical background of this study: patterns of life-history traits vary not only among higher taxonomic levels, but also among species and individuals and, within certain limits, even among single stages of individual life cycles and with age. Phenotypes of life-history traits are not generally fixed, but rather plastic permitting individuals to respond to environmental conditions and short-term changes (Stearns 1992, Ricklefs 2000, Martin 2004). This phenotypic plasticity has several implications for breeding ecology and breeding success of individuals as well as for demography and population ecology. Breeding performance of individual birds potentially varies between seasons. It is shaped by several individual decisions and compromises on if, where, when and how to breed in order to achieve maximal fitness by reproducing successful and by maintaining simultaneously (or at least alternatively in long-lived species) the chance to survive to the next breeding season.

On the basis of examples, the following section gives a short overview about the questions on which environmental factors induce such “compromises”, how individuals decide under given conditions, which life-history traits are concerned and how breeding success is affected. The description concentrates mainly on long-lived species such as gulls and waders, these being similar to those addressed in this thesis.

1.2. Annual breeding success: Individual decisions and constraints

Prior to or during each breeding season, birds have to decide whether and when to breed (timing of breeding), where to breed (habitat and nest-site selection) and how to breed (competition with conspecifics, reproductive effort) to achieve maximum breeding success and to guarantee survival to the next breeding season. However, optimal annual breeding performance is not only a product of individual decisions. Birds are potentially simply constrained to accept some traits of their performance, including offspring survival and current reproductive output. As shown by the examples given below, these constraints are based on distinctive environmental stochasticity affecting predictability of spatial and foraging resources and on the individual phenotypic quality of breeding birds (physiological and health condition, age and experience).

1.2.1. Effects of timing of breeding and habitat selection

Breeding early in the season in birds is commonly assumed to increase post-fledging survival and fitness by increasing experience, social status, body condition, etc. of offspring (see Nilsson 1999 for a review). But even short-term advantages of early breeding are conceivable through temporally avoiding periods of high nest predation pressure or kleptoparasitism (Götmark 2002, Arnold *et al.* 2004). Besides effects of timing of breeding *per se*, effects of timing of breeding should be seen within the framework of habitat and nest-site selection. In general, habitat and nest-site selection is a behavioural response to different proximate factors used as cues to the ultimate factors of habitat selection including optimal protection from weather and predation and accessibility to food resources. The ultimate aim of habitat selection is to satisfy specific requirements as widely as possible to achieve optimal breeding success (Hildén 1965, Cody 1985, Jones 2001). An optimal habitat and nest-site promising a high breeding success should be expected when individuals can really select freely, when individuals assess proximate cues correctly and when conditions such as food availability and predation risk are reasonably predictable. These assumptions should rarely be completely realisable under natural conditions. Positive consequences of habitat selection for breeding success should rather depend on early arrival at the breeding site (that itself is constrained by body condition, age and experience of individuals, e.g., Summers & Underhill 1991, Kokko 1999, Forstmeier 2002, Smith & Moore 2003, Dittmann & Becker 2003) and the competitive ability of individuals as well as environmental factors related to habitat and population density.

Under the condition of limited spatial resources of varying reproductive quality, it indeed pays for individuals to arrive early to occupy vacant high quality territories. Territorial birds usually occupy habitats of relatively high reproductive value first, with a higher density and with positive consequences for breeding success. This behaviour leads to an uneven distribution of breeding pairs on habitats as predicted by theory on “ideal free” and “ideal despotic distribution” (Fretwell 1972, Bernstein *et al.* 1991, Sutherland 1996). Though, what are the major factors discriminating “good” from “bad” territories and promoting a “despotic distribution” of territorial birds with crucial consequences for breeding success? It is a well known phenomenon in several wader species that birds are densely distributed near foraging sites but less densely remote from these sites (e.g., Lauro & Burger 1989, Ens *et al.* 1992, Valle & d'Este 1994, Milsom *et al.* 2000, 2002) suggesting that food supply may be one component promoting a despotic distribution. One of the most prominent examples of breeding success and fitness consequences of this distribution is that of Oystercatchers *Haematopus ostralegus* breeding on a Dutch Wadden Sea island (Ens *et al.* 1992, 1995, Heg 1999): owing to direct access to food for parents and offspring, pairs breeding as “residents” next to tidal flats achieve significantly higher breeding success than those breeding as “leapfrogs” at a distance from the flats. Constrained by high population density, birds may have to decide whether to breed at all in habitats of low reproductive quality or to become a non-breeding floater that "queues" by refraining from breeding until a high quality territory is vacant (cf. Zack & Stutchbury 1992, Sutherland 1996, Kokko & Sutherland 1998). Both strategies may be evolutionary stable: due to a relatively longer reproductive lifespan, "leapfrogs" breeding at an early age in low quality habitats achieved a lifetime reproductive success similar to that of "residents" breeding relatively old in high quality habitats with high annual breeding success (Ens *et al.* 1995, but see Heg 1999 for effects of individual quality). Regardless of such strong evidence, habitat suitability should generally not be determined by food availability alone. Birds should rather have to trade-off between the risk of predation or human disturbance and food accessibility during the selection of an appropriate breeding habitat. As reported, for example, by Burger (1985), Møller (1991), Berg *et al.* (1992), and Tryjanowski *et al.* (2002), habitat and nest-site selection and the resultant breeding success are affected by the incidence and activity of predators. Even the organisation of a colony of, for example, gulls and terns should be explainable by predation risk. Experienced birds which occupy a nest-site in the centre of the colony are usually less susceptible to predation (e.g., Patterson 1964, Furness & Monaghan 1987, Becker 1995; but see Brunton 1997).

Given a despotic distribution in territorial breeding birds, the temporal and spatial distribution of habitat and nest-site occupation should reflect habitat quality and breeding success, regardless of the decisive proximate and ultimate factors of habitat occupation. However, responding to, for example, predator occurrence and food availability by habitat selection requires existence and accurate assessment of proximate cues by selecting individuals prior to territory occupation and breeding. False assessment of proximate cues can lead into a so-called "ecological trap" characterised by high attractiveness (e.g., owing to high food abundance) but low reproductive quality (e.g., owing to high predation) (see 1.3.). Examples of ecological traps range over a variety of species and habitats (see examples in, e.g., Kokko & Sutherland 2001, Battin 2004). Evidence was also found in breeding waders (Witt 1986, Galbraith 1989, Székely 1992, Thyen & Exo 2003).

1.2.2. Effects of food limitation and weather

Availability and accessibility of food is, of course, a fundamental factor that birds have to consider during habitat selection to breed successful. However, as described above, individuals cannot completely resolve the problem of providing a sufficient food supply for parents as well as offspring by simply selecting a suitable place to breed. They rather have to trade off constraints such as competition for prey, seasonality of prey abundance, population dynamics of prey, temporal food shortage caused, for example, by weather, etc. Although additionally affected by parental condition, age and experience, food limitation is actually an important factor which birds have to trade-off during reproduction leading to an adjusted resource allocation among body condition and different reproductive traits and, thus, to varying breeding success. Reduced clutch or egg sizes as a response to limited food resources are reported for several larid species (Becker *et al.* 1985, Ratcliffe *et al.* 1998, Kitaysky *et al.* 2000, Clifford & Anderson 2001) as well as for waders (Blomqvist & Johansson 1995, Amat *et al.* 2001b, Flodin & Hirsimäki 2004). Since reduced clutches naturally reduce the number of potential fledglings, and since chicks that hatch from small eggs suffer a relatively low survival (e.g., Lundberg & Väisänen 1979, Galbraith 1988, Hegyi 1996, Amat *et al.* 2001a), both phenomena impair breeding success and recruitment. In extreme situations, birds may even refrain from egg production or cease current breeding events (Calladine & Harris 1997, Erikstad *et al.* 1998, Bradley *et al.* 2000, Verboven & Tinbergen 2002). Food shortage may additionally affect resource allocation within an individual brood. As shown in recent studies, it may be advantageous under unfavourable foraging conditions to reduce parental effort by producing daughters instead of more costly sons, whose energy requirements are higher during development. This may be particularly true in species with altricial or semi-precocial young and sexually size-dimorphic offspring such as many larid species (Nager *et al.* 2000b, Daunt *et al.* 2001, Alonso-Alvarez & Velando 2003). Limited resources may additionally constrain parents to sacrifice less competitive (mostly smaller and/or female) siblings of a brood (Royle 2000, Nager *et al.* 2000a, Heg & van der Velde 2001, Amat *et al.* 2001b, Becker & Wink 2003).

In addition to exploitation by humans or intraguild competitors and interference competition, diverse weather factors may be among the most important causes of temporary food shortage. Effects of low winter and spring temperatures and effects of high precipitation on breeding performance of northern hemispheric larids and waders may provide well studied examples. Low temperatures may affect development, vertical distribution and activity of aquatic and endobiotic prey leading to a reduced food availability (Becker & Specht 1991, Beukema *et al.* 2000, Armonies *et al.* 2001). Rain may impair prey visibility for surface feeding aquatic birds (Becker *et al.* 1985, Becker & Specht 1991), but may enhance activity and availability of epibiotic and endobiotic prey of birds feeding terrestrially or intertidally (Pienkowski 1983a, Edwards & Bohlen 1996, Frampton *et al.* 2000). Moreover, weather factors constrain parents not only to trade off several traits of parental effort including offspring production and provisioning (see above) but also direct effects on chick survival. Temperature and rain may cause hypothermia and death or retarded growth of chicks, preventing being unable of independent thermoregulation several days after hatching (Beintema & Visser 1989a, Becker & Specht 1991, Visser & Ricklefs 1993, Hötker & Segebade 2000).

1.3. Annual breeding success: from individuals to populations

Population growth rates are basically determined by four main demographic parameters interacting in the fashion (recruitment + immigration) – (mortality + emigration) (e.g., Begon *et al.* 1997, Sibly *et al.* 2003). The relationship between individual life-history, breeding success and population size and growth is consequently quite obvious. Apart from personal maturation and survival, each individual of a breeding population contributes to future population size by its fecundity which determines the number of potential recruits. The intrinsic growth rate of a population, i.e. the asymptotic growth rate, is species-specific. It is ultimately determined by the trade-off elucidated in the section above, i.e. the trade-off between reproductive capacity and survival (Sibly & Hone 2003, Sinclair & Krebs 2003). From these principles, it is clear that the demographic parameters are of varying importance for population dynamics in different species characterised by different life-history strategies. Populations of “slow species” (small clutches, high survival) are more sensitive to adult survival which contributes to a relatively higher extent to future population size than in “fast species” which in turn are more sensitive to breeding success and recruitment (Croxall & Rothery 1991, Sibly & Hone 2003, Reid *et al.* 2004). This fact is of crucial importance in understanding and modelling population dynamics and in combined monitoring of demographic parameters (Croxall & Rothery 1991; see below).

However, intrinsic growth rates of populations should very rarely be realised in natural populations. Populations should rather numerically respond to several density-dependent (leading to population regulation) or environmental factors (e.g., food, breeding space, predation) causing population fluctuations (Newton 1998, Sinclair & Krebs 2003, Sutherland & Norris 2003). Compared to many other taxonomic groups, population dynamics of birds are fairly complex. Birds are relatively long-lived, most are highly mobile, frequently migratory and occupy a wide range of habitats. Density-dependent mechanisms and environmental factors can act on each of the demographic parameters mentioned above. The effects may vary by age, by stages within the annual life-cycle (breeding, migration, wintering) and by spatial distribution (Perrins *et al.* 1991, Sutherland 1996, Newton 1998, Sibly *et al.* 2003). As shown in several wader and larid species, mortality of subadults until maturation and recruitment is considerably higher than in mature birds. For example, first-year mortality of Redshanks *Tringa totanus* is estimated 55 % and 36 % in Oystercatchers, whereas adult mortality ranges from 30 % in Redshank to 14-30 % in Oystercatchers (Boyd 1962, Insley *et al.* 1997). In Black-headed Gulls *Larus ridibundus* and Herring Gulls *L. argentatus*, estimations of first-year mortality range from 40 to 60 %, that of adults 15 to 40 % (Flegg & Cox 1975, Glutz von Blotzheim & Bauer 1999a). In Common Terns *Sterna hirundo*, Becker *et al.* (2001) report a subadult return rate of 35 % (suggesting a subadult mortality of up to 65 %) compared to an adult return rate of 91 %. Causes for this age-dependently varying mortality are assumed to be later migration, less experience and less competitive ability of younger birds resulting in less successful predator avoidance and less access to favourable food resources (e.g., Evans 1991, Cresswell 1994, Sutherland 1996). In migratory birds, highest mortality occurs during migration and wintering because of high energetic costs (migration, thermoregulation), high competition and food exploitation at wintering and stopover sites, and unpredictability of foraging and weather conditions during the non-breeding season (e.g., Evans *et al.* 1984, Evans 1991, Piersma 1994, Wiersma & Piersma 1994, Newton 1998, Battley *et al.* 2001, Le van Dit Durell *et al.* 2001, Goss-Custard *et al.* 2001, Green *et al.* 2004). Mortality during migration and wintering depends widely on the migration strategy performed by a species or population. Mortality during the non-breeding season is consequently space-dependent at large (e.g., temperate vs. tropical wintering grounds; see Piersma 1994, Scheiffarth 2003) as well as at small spatial scales (e.g., different stopover sites within ecosystems; see Whitfield 1988, Camphuysen *et al.* 1996).

Thus, mortality of immature and adult birds varies seasonally. In many species, highest mortality occurs during migration and wintering. Mortality appears actually to be lowest during the breeding season (however, the Herring Gully and the Black-headed Gull may be exceptions; see Glutz von Blotzheim & Bauer 1999a) when, instead, breeding success as further important demographic parameter varies by a wide range of influencing factors as elucidated in the sections above. It is a well known phenomenon in population ecology that population number respond to the factors described: theoretically, “positive factors” cause an increase in population size by increasing breeding success or reducing mortality until carrying capacity is achieved. At carrying capacity, population growth rate is near zero and populations may be regulated by density-dependence (Perrins *et al.* 1991, Sutherland & Norris 2003). Apart from some simulation studies (e.g., Oro & Ruxton 2001, Amarasekare 2004), migratory processes between populations or subpopulations including its influencing factors are far less studied than breeding success and mortality (Clobert & Lebreton 1991). Emigration and immigration may be negligible in equilibrium populations in which long-term recruitment balances long-term mortality. However, there is evidence from several studies that apparently stable populations can even be sustained by immigration (rather than by recruitment) from populations which itself are stable and sustained by recruitment and dispersal (e.g., Murphy 2001, Perkins *et al.* 2003, Battin 2004, Müller *et al.* 2005). Respective populations are connected by so-called “source-sink-dynamics” (Pulliam 1988, With & King 2001, Amarasekare 2004). Source-sink dynamics are often driven by individual decisions in habitat selection as mentioned above (Remes 2000, Delibes *et al.* 2001, Kristan 2003, Battin 2004). The mal-assessment of reproductive quality of habitats may lead to insufficient reproduction and, consequently, recruitment. These “sink populations” in highly attractive habitats wrongly assessed as high in quality for reproduction are replenished by immigrants attracted from “population sources” in which population growth is positive (Pulliam 1988). Changes in population size used as indicators in several monitoring programmes are, thus, not obvious in each case but can rather be masked by small-scaled spatial population dynamics (Battin 2004, Bock & Jones 2004).

1.4. Aims and organisation of the thesis

1.4.1. Inspiration of the study

The European Wadden Sea is an abundantly populated breeding area of coastal bird species including waders, gulls and terns. The Wadden Sea breeding population of Black-headed Gulls, Herring Gulls and Common Terns comprise about 10 % of their respective total NW European population. The ecosystem is even more important for several wader species. About 20 % of the NW European population of Oystercatchers and Redshanks and more than 50 % of the respective Avocet population breed within the Wadden Sea area (Hagemeijer & Blair 1997, Rasmussen *et al.* 2000). Most of these species experienced a remarkable and specific population development during the last century or at least during the elapsed decades. Black-headed Gulls still bred only at inland breeding sites in the first half of the 20th century and settled the German Wadden Sea during the 1930s. It is currently the most abundant breeding bird species of the Wadden Sea (Vauk & Prüter 1987, Garthe *et al.* 2000, Südbeck & Hälterlein 2001). The Wadden Sea breeding population of Herring Gulls declined during the first half of the 20th century but increased exponentially until the 1980s and have been at equilibrium levels in recent years (Vauk & Prüter 1987, Garthe *et al.* 2000). At the southern North Sea coast, Common Terns were most abundant at the beginning of the 1980s, but declined until the middle of the 1990s. In contrast, the population was stable in northern parts of the Wadden Sea during the same period (Südbeck *et al.* 1998). The breeding population of Oystercatchers increased during the 1980s and 1990s, whereas populations of Avocet and Redshank were stable during that period (Hälterlein *et al.* 2000).

In case of the Redshank, this population trend is completely different from that of most European inland breeding sites (e.g., Tucker & Heath 1994, Melter & Welz 2003) and even of British saltmarshes (Norris *et al.* 1998) where Redshank populations are in sharp decline.

What might be the causes for these high breeding densities of several coastal bird species as well as stable or even increasing populations? Supply, availability and suitability of habitats are highly unpredictable for breeding birds within the Wadden Sea area. Availability of fish for piscivorous birds and of invertebrates for benthos predators such as waders and gulls is highly unpredictable due to factors such as weather conditions (described above). Dune and saltmarsh habitats are exposed to rapid changes due to wind, tidal flooding and vegetation succession. These phenomena potentially cause short- and long-term losses of breeding habitats leading to abandonment and recolonisation of breeding sites. Catastrophic weather or flooding events can even lead to total losses of broods during some years (Becker & Anlauf 1988*a*, Evans 1991). Despite these apparently inhospitable conditions, the Wadden Sea is nevertheless an obviously attractive breeding area for coastal birds. All coastal bird species mentioned above are adapted to these conditions by “slow” life-histories. Its populations are consequently relatively unsusceptible to irregular breeding failures (see above). In addition, the Wadden Sea ecosystem is highly productive suggesting a high food supply. Its potential habitat structures are diverse, spacious and relatively undisturbed owing to a relatively low accessibility of breeding habitats on islands and in wetlands and owing to several conservation measures since the beginning of the 20th century (Exo 1995, NPA & UBA 1998, NLP-V & UBA 1999, Exo *et al.* 2003).

Several studies on foraging ecology and habitat selection emphasise that food supply and low disturbance may be a major reason for the a high attractiveness of the Wadden Sea for breeding coastal birds (e.g., Vauk & Prüter 1987, Brandl & Gorke 1988, Gorke 1990, Joest 2003). However, apart from few exceptions (Oystercatcher: e.g., Ens *et al.* 1992, Heg 1999; Avocet: e.g., Hötker & Segebade 2000, Hötker 2000; Common Tern: Becker 1998, Becker *et al.* 2001), fitness consequences or, at least, consequences for reproductive success of breeding in the Wadden Sea are rarely studied. For most species and for most regions, it is not known how successfully birds breed annually and in the long-term. It is not known, which major influencing factors determine breeding success and how breeding success is actually affected by food supply, habitat and nest-site selection, and disturbance. In addition, it is not known how potentially positive influencing factors such as high food supply, suitability of habitats and low disturbance are counteracted by predation, introduction of predators on islands, high breeding densities of birds, etc. In particular it is not known how the high breeding densities and population trends mentioned above can be explained. It has to be assumed *a priori*, that high abundances and stable or increasing trends are supported by high breeding success due to favourable food and spatial resources. But, apart from the exceptions given above, this assumption has never been tested, least of all spatial variability of reproduction.

1.4.2. Aims of the study

The present study was inspired by these open questions. It was conducted on the coastal bird species mentioned previously representing high abundant breeding bird species, occupying a variety of different habitats and representing different foraging ecologies and different life-history strategies. The populations of the studied species are unequally distributed on islands and mainland of the Wadden Sea. Pairs of Common Terns, gull species and Oystercatchers breed mainly on islands, those of Avocets and Redshanks mainly at the mainland coast near muddy tidal flats (Rasmussen *et al.* 2000). Common Terns forage largely on fish (Glutz von Blotzheim & Bauer 1999b, Becker & Ludwig 2004), Black-headed Gulls and Herring Gulls forage opportunistically on, e.g., benthos, fish and even waste (Vauk & Prüter 1987, Wilkens & Exo 1998, Glutz von Blotzheim & Bauer 1999a). The waders feed mainly on tidal flat invertebrates (Glutz von Blotzheim *et al.* 1986, 1999). Except for Redshank, all species mentioned are open-nesting. Avocets and larids breed in colonies. The young of gulls and terns are semi-precocial, those of waders precocial. Except for Redshanks and Avocets, chicks of the species mentioned are fed by the parents until fledging (Glutz von Blotzheim *et al.* 1986, 1999, Glutz von Blotzheim & Bauer 1999a, 1999b).

In detail, this study aimed to:

- determine **hatching and breeding success of coastal bird species and associated spatial variability** within the German Wadden Sea area as well as to evaluate hatching and breeding success against the background of recent population trends. It was hypothesized that breeding success was high in most species and at most breeding sites. For species with increasing populations, it was predicted that breeding success was greater than that needed to sustain equilibrium population size.
- determine **effects of selected potentially influential factors** (weather and habitat selection) on selected reproductive traits of coastal birds.

  Effects of weather on breeding success and chick development were studied on Black-headed Gulls as model species. Whereas population development and foraging ecology is well known in this species, breeding success was never previously studied in the Wadden Sea (but see Stienen *et al.* 1998). Medium-term data on breeding biology originating from the 1990s are analysed in detail. Considering potential negative effects on food supply known from literature, it was hypothesized that a severe winter during the study period affected Black-headed Gull reproduction. It was furthermore supposed that more current weather phenomena (rain, temperature and wind during breeding performance) had more direct additional effects on breeding success and chick development.

  Effects of several habitat and nest-site parameters on hatching success and nest predation were studied on Redshank as model species. In contrast to most other coastal birds, this species breeds non-colonially in well concealed nests. It therefore was supposed that hatching success and nest predation is largely dependent on several habitat and nest-site parameters (topography, vegetation). It was hypothesized that hatching success varies among saltmarsh habitats distinguished by topography and vegetation. Due to lower predation, a relatively high hatching success was predicted for well structured habitats and nest-sites located in plant communities of advanced stages of the saltmarsh chronosequence.

- verify the suitability of the trilaterally agreed **methodology on monitoring breeding success of coastal birds** in the field (Exo *et al.* 1996) and to evaluate the explanatory power of the results according to the targets of the programme, i.e. to determine “natural breeding success”, to evaluate responses of indicator species to environmental changes (“early warning system”) and to derive negative environmental impacts from variation in hatching and breeding success (Trilateral Monitoring and Assessment Group 2000). It was hypothesized that different breeding locations and different breeding bird species with different life-histories and different ecologies are needed to achieve the aims of the programme. It was predicted that a well advised choice of breeding sites and indicator species should permit conclusions to be drawn on the effects of, amongst others, human disturbance, agriculture, food supply and pollution in different compartments of the ecosystem.

All of the studies mentioned are recently published or accepted for publication. Sections 2. to 4. are addressed to selective influencing factors using single representative species. Section 5. comprises the results of a two year pilot study conducted in 1996/1997 within the total Wadden Sea area of Germany including five coastal bird species. Spatial variability and the potential role of current reproduction for population dynamics (sections 1.5. and 1.6.) are assessed by considering all studies mentioned. Sections 1.7. to 1.9. resume the results and conclusions of the single publications.

1.5. Spatial variability of coastal bird reproduction

As suggested by the results recorded at 17 breeding sites throughout the German Wadden Sea, coastal bird reproduction is spatially variable. This variability is largely explained by small scale and short-term variation in occurrence of predators (possibly mostly Red Foxes *Vulpes vulpes*) and flooding. Catastrophic breeding failures of Common Terns breeding at the Jadebusen, of Oystercatchers on Langeoog island and those of Avocets breeding at Schobüller Bucht each in 1996 serve as examples (see section 5.). Additionally, there are obviously some low-lying breeding sites along the mainland coast where flooding causes high or even total breeding failures quite regularly (e.g., Schobüller Bucht and Norderhever Koog in Schleswig-Holstein; cf. Becker & Anlauf 1988b). However, there are obviously even more general spatial trends in coastal bird reproduction which may be related to specific behaviour including feeding and habitat selection. Intersite differences are thus ultimately explained by food and spatial resources used by breeding birds in the Wadden Sea in a specific manner.

Hatching and breeding success of birds appears to be higher on islands than at the mainland coast. Except for Black-headed Gulls, egg as well as chick predation of all species studied at different breeding sites was relatively low on the islands. As shown in a recent study, this is even true in Redshanks (Thyen *et al.* 2005). Breeding on islands is assumed to be advantageous due to usually relatively low densities of mammalian predators (Nettleship *et al.* 1994). Though, this advantage is frequently counteracted by the colonisation by, or the introduction of small mammalian predators such as Hedgehogs *Erinaceus europaeus*, rats and feral cats in particular on inshore islands (Burger & Gochfeld 1994, Jackson & Green

2000, Nordström & Korpimäki 2004). On Wadden Sea islands, mammalian predator communities are indeed different from those of the mainland. For example, Red Foxes and mustelids are absent on most East Frisian Islands (Bröring *et al.* 1993) whereas they should occur at most mainland breeding sites. In contrast, Hedgehogs, Common Rats *Rattus norvegicus*, and Wood Mice *Apodemus sylvaticus* are common on most East Frisian Islands (Bröring *et al.* 1993) being presumably responsible for breeding failures of Black-headed Gulls on Langeoog in 1996/1997.

Based on the mechanisms on maximisation of breeding success by habitat selection (see above) (Lack 1968), even the comparatively high breeding densities on islands as mentioned above could be explained by relatively low predation pressure on islands. Owing to their preference for muddy sediments as feeding sites, Avocets and Redshanks may be constrained to breed at the mainland coast where muddy intertidal areas are more extensive (Ragutzki 1982, Reineck 1982). However, despite obviously lower mammalian predation in most species, breeding success is not inevitably higher on islands as shown by the example of Common Terns (see section 5.). Although this phenomenon was not observed during this study, island-breeding terns frequently suffer breeding failures due to intensive predation by coexisting Herring Gulls (Becker 1984, Becker 1995). Additionally, as supply of marine food depends on the tide and particularly in years with unfavourable foraging conditions, it appears to be advantageous for terns to breed at the mainland where consistent limnetic food supplies can be used as alternative feeding sites (Frank 1992, Becker *et al.* 1997c). A similar alternative or supplemental feeding can be assumed for Black-headed Gulls breeding at the mainland coast (see section 2.).

1.6. Spatial and temporal population dynamics: potential role of current reproduction

To assess current breeding success with respect to time, space and population dynamics, several preconditions should be met. These conditions mainly originate from spatiotemporal variability of breeding success in unpredictable environments such as the Wadden Sea and from variability of further demographic parameters depending on breeding habitat selection and migratory behaviour of a population. Ideally, the former problem should be overcome by long-term studies permitting an estimation of long-term breeding success for a regional breeding area. To assess the contribution of breeding success to population dynamics, minimum breeding success needed to sustain equilibrium population is an appropriate measure. The calculation of this measure, however, requires an accurate knowledge of further demographic parameters of the population concerned, i.e. age at first breeding, age-specific mortality and recruitment rate. Reference populations from which demographic parameters are derived should be comparable in breeding habitat, migration route and distance, and location of stopover and wintering sites.

Owing to an ecosystem-wide programme on monitoring breeding birds in the Wadden Sea (see below; e.g., Hälterlein & Südbeck 1996, Rasmussen *et al.* 2000), current population sizes and temporal population dynamics are relatively well known in most coastal bird species. In contrast, current knowledge of further demographic parameters permitting to derive minimum breeding success as elucidated above is only available for a very limited number of species, i.e. Common Tern (Wendeln & Becker 1998, Becker *et al.* 2001), Oystercatcher (Schnakenwinkel 1970) and Avocet (Hötker 1999, Hötker & Segebade 2000).

Except for Black-headed Gulls, most studies presented in this thesis were conducted in a short-term. Nevertheless, as elucidated in section 5, data (including those on chick development in the larids) should permit the conclusion, that breeding success was relatively low in 1996 (except for Herring Gulls) and on an average level in other study years. Black-headed Gulls and Common Terns suffered relatively low success in 1996 due to food-shortage, weather and interactions among these factors. The same may be true to a certain extent for Oystercatchers and Avocets which additionally experienced high offspring losses due to predation and flooding. Redshank breeding at the Jadebusen suffered very high egg losses due to predation in 1997 as well as in 2000/2001 (see sections 3. and 4.).

In most species, the observed breeding success supports the population trends mentioned above. Median reproductive output of **Common Terns** in 1996/97 was 0.6 fledged chicks * pair^{-1} (range: 0.0 to 1.3). As calculated by Wendeln & Becker (1998) for a Wadden Sea colony, minimum breeding success required to sustain equilibrium population is about 0.8 fledglings * pair^{-1}. Being locally high but altogether rather low, current breeding success may therefore support decreasing and regionally stable populations during the 1990s in the German Wadden Sea (Südbeck *et al.* 1998). A twelve-year average breeding success of 0.4 fledglings * pair^{-1} achieved on the Dutch Wadden Sea island of Griend reported by Stienen & Brenninkmeijer (1998) and an output of 0.7 fledglings * pair^{-1} (Becker *et al.* 1997a) in the 1993-1995 period may additionally support this appraisal (but see Frank (1998): 1.0 fledglings * pair^{-1} on Baltrum island in 1993-95).

The **Herring Gulls** studied in their biggest German colonies on Langeoog and Mellum island, consisting of about 16,000 breeding pairs in 1997 (Südbeck & Hälterlein 1999), achieved a consistently high breeding success ranging from 0.8 to 1.5 fledglings * pair^{-1} in both spatial and temporal terms. Assuming that parameters are transferable to Wadden Sea colonies, minimum breeding success derived from UK populations during the 1960s should be 0.6 fledglings * pair^{-1} * year^{-1} (Glutz von Blotzheim & Bauer 1999a). Thus, minimum success was exceeded in all study years in both colonies, suggesting an inconsistency with the current equilibrium population (Garthe *et al.* 2000). Since the 1960s, population development of Herring Gulls was similar in both the Dutch and the German parts of the Wadden Sea. It was characterised by an exponential population growth during the 1960s and 70s until the middle of the 80s and equilibrium population till the 1990s (Becker & Erdelen 1987, Spaans *et al.* 1987, Becker & Exo 1991, Garthe *et al.* 2000). In accordance with this population development, a decrease in annual breeding success from 1.4 fledglings * pair^{-1} in the 1960s to 0.4 fledglings * pair^{-1} in the 80s (Spaans *et al.* 1987) and 0.5 fledglings * pair^{-1} in the 90s (Bukacinska *et al.* 1996) was found in the Netherlands. This decrease in breeding success is attributed to density-dependent population regulation driven by food shortage and cannibalism (van Klinken 1992, Brouwer & Spaans 1994, Bukacinska *et al.* 1996). Interestingly, breeding success remained remarkably stable in the German Wadden Sea colonies during the same period (Becker & Exo 1991, Wilkens & Exo 1998, Glutz von Blotzheim & Bauer 1999a). This unchanged high reproductive output may be largely explained by the extensive use of rubbish dumps as a food source (Wilkens & Exo 1998). However, since winter mortality of the gulls may even be lowered by the usage of dumps

(Bellebaum *et al.* 2000), dispersal, emigration and floating may be the only plausible explanations of the observed population development.

Black-headed Gulls have displayed a considerable breeding range expansion in Europe since the 19th century, including the settlement of the German Wadden Sea in the 1930s (Vauk & Prüter 1987, Hagemeijer & Blair 1997). While recently declining at German and Dutch inland sites and even in the Dutch Wadden Sea (van Dijk 1998, Stienen *et al.* 1998, Bellebaum 2002), the German Wadden Sea population was still increasing during the 1990s (Garthe *et al.* 2000, Bellebaum 2002). Breeding success of Black-headed Gulls was relatively constant varying between 0.6 and 0.8 fledglings * pair^{-1} at the Jadebusen during 1994-1997 (see section 2.). This ranged from 0.1 to 1.6 fledglings * pair^{-1} (median 1.2 fledglings * pair^{-1}) on the Schleswig-Holstein mainland during 1995-1997 (see section 5). Unfortunately, no attempt at an integrated population study has presently been made to explain breeding range expansion and spatially varying population trends (but see Starke 1982, Stienen *et al.* 1998). However, considering data on subadult mortality (0.64 in the first three years of life) originating from SE England (Flegg & Cox 1975) and an adult mortality of 0.1 as given by Prévot-Julliard *et al.* (1998) for a French colony, minimum breeding success should be about 0.6 fledglings * pair^{-1} * year^{-1} to sustain equilibrium population (as calculated according to Henny 1972). The annual breeding success presented in this thesis may, thus, explain population increase in the German part of the ecosystem. Though, breeding success may not explain population development differing between the German and the Dutch part of the Wadden Sea: the population of the latter achieved a similar reproductive output in 1997 (i.e. 0.7 to 1.4 fledglings * pair^{-1}) (Stienen *et al.* 1998).

The population of **Avocets** breeding in the German Wadden Sea increased until the 1980s and was highly variable, but without directional trends during the 1990s (Hälterlein *et al.* 2000). Considering the estimation of Hötker (1999) of subadult (0.78) and adult mortality (0.17), minimum annual breeding success of 1.5 fledglings * pair^{-1} should keep an equilibrium population. Given the mortality rates reported by Glutz von Blotzheim *et al.* (1985) (0.6 vs. 0.28), minimum breeding success ranges in the same order of magnitude. This value was never achieved at any of the studied colonies during 1996/97 (median: 0.1, range: 0-0.8), mostly due to flooding, egg predation and weather during chick rearing (cf. Hötker & Segebade 2000). Even in the long-term (1988-1997), average annual breeding success was 0.4 fledglings * pair^{-1} and thus probably far too low to maintain regional population size. It therefore has to be questioned how the population development mentioned above has to be explained. High annual variability in population size may be the result of variability of breeding success owing to catastrophic breeding failures. However, why is the Avocet population generally stable? During the 1990s, emigration of Wadden Sea breeding birds to other European breeding sites was observed (Hälterlein *et al.* 2000) possibly indicating saturation of Wadden Sea breeding habitats. Although flooding and weather may be the most important factors, density-dependent bottom-up mechanisms may additionally reduce reproductive output. Emigration and relatively high dispersal (Hötker 1999) hamper an accurate assessment of mortality rates. It, thus, has to be additionally considered that minimum breeding success derived from mortality rates could actually be lower than that given above.

The Wadden Sea breeding population of **Oystercatchers** has increased for several decades, probably owing to eutrophication and a resultant enlargement of the benthic food supply (Rasmussen *et al.* 2000, Hälterlein *et al.* 2000). However, population development varied regionally. During the 1990s, the population significantly increased in the German part of the Wadden Sea whilst decreasing in the Dutch part caused by severe winter weather and man-made overexploitation of mussel beds leading to an increased winter mortality (Rasmussen *et al.* 2000). Median hatching success of Oystercatchers studied during 1996/1997 was 30 % of clutches and ranged from 1 to 97 %. Clutch size of Oystercatchers is 3 eggs (Glutz von Blotzheim *et al.* 1999), chick mortality until fledging is 30 % as reported from the Dutch Wadden Sea island of Schiermonnikoog (Jager *et al.* 2000), and minimum annual breeding success required to maintain a stable population is 0.4 fledglings * pair^{-1} (as derived from mortality data given by Schnakenwinkel 1970 and Wolf 1998). Considering these data, a minimum annual hatching success of about 44 % should be achieved to provide a sufficient breeding success. This value should mostly be significantly exceeded on islands and even in years and at breeding sites when and where no catastrophic flooding events occur (see Fig. 5.3). Based on long-term data of Hälterlein (unpubl., see Fig. 5.13), minimum hatching success should regularly easily be exceeded at some breeding sites (such as Westerhever) but similarly be regularly much lower at other sites (such as Norderhever Koog). This phenomenon suggests a high spatial variability of Oystercatcher reproductivity in the Wadden Sea. Against this background, similar to Redshanks (see below), large-scale increase of breeding populations may possibly be the product of distinct source-sink dynamics. Development of the Oystercatcher population breeding in the Dutch Wadden Sea as mentioned above is assumed to be based on an increased winter mortality. Additionally, a rather low long-term (1984-1995) annual breeding success of 0.1 to 0.5 fledglings * pair^{-1} is reported from Schiermonnikoog (Ens *et al.* 1992, Heg & van der Velde 2001). However, it does not explain if this relatively low breeding success is a cause for decreasing populations or a consequence of low food supply due to food exploitation and high breeding density on the island (see Ens 1992, Heg 1999).

The north-western and central European **Redshank** breeding population has drastically declined during recent decades due to agricultural intensification and loss of mainly inland habitats (Tucker & Heath 1994, Bauer & Berthold 1996). Whereas in Britain a decline is recorded even in saltmarshes (Norris *et al.* 1998, Brindley *et al.* 1998), the Wadden Sea breeding population is still stable on a relatively high level (Rasmussen *et al.* 2000, Hälterlein *et al.* 2000). Even in the western Jadebusen including the study areas (see sections 3. and 4.), the Redshank population is stable since at least 1990 (Thyen & Exo 2001) suggesting *a priori* a sufficient reproduction and recruitment. However, assuming a minimum breeding success of 0.7-1.0 fledglings * pair^{-1} required to maintain current population size (as estimated by den Boer (1995) at Dutch inland breeding sites), a pre-fledging mortality of 50% as estimated by Großkopf (1959) on Wangerooge island and a clutch size of 4 eggs, a minimum annual hatching success of 35-50 % is required to guarantee a sufficient reproduction. Hatching success recorded in 1997 and 2000/2001 ranged from 10 to 28% and should thus not provide a sufficient annual reproductive output. This is true even for the 2000-2004 period (Thyen & Exo 2005). Although, as with Oystercatchers (see above), Redshank reproduction appears to be distinctly spatially variable within the Wadden Sea ecosystem. On Wangerooge, Großkopf (1989) found an average hatching success of 77% during 1955-1958. More recently, Büttger (2004) reports a hatching success of about 90% in 2003 on the same study area. Given long-term equilibrium populations at both study sites, the Wangerooge breeding population potentially could represent a source population whilst that of the Jadebusen possibly is a sink population within the Wadden Sea. The latter may even be an “attractive sink habitat” and, thus, an ecological trap (Thyen & Exo 2003, Battin 2004, Thyen *et al.* 2005).

1.7. Effects of weather on coastal bird reproduction

As elucidated in earlier sections, weather affects reproduction of birds through a variety of mechanisms by influencing, amongst others, timing of breeding, food supply and availability, chick development and pre-fledging survival. Within the limits of their specific phenotypic plasticity, certain weather events such as low temperature, rain and wind can constrain birds to adjust resource allocation among somatic and reproductive traits to the given conditions. In birds preying upon pelagic food, it has been shown that rain as well as wind can impair foraging by diminishing food availability (Becker & Specht 1991, Frank 1992, Finney *et al.* 1999, Stienen *et al.* 2000). Detectability and availability of prey of benthos predators increase by substrate moisture and therefore rain (though rainfall may impair visibility of active polychaetes), but is minimised by wind and cold temperatures owing to variation in benthos activity (Pienkowski 1981, 1983a, 1983b, Evans 1987). Similarly, availability of terrestrial invertebrates is affected by rain and temperature (Edwards & Bohlen 1996, Frampton *et al.* 2000). Thus, notwithstanding the direct effects of temperature, rain and wind on chick development and survival by affecting thermoregulation of the young (e.g., Visser & Ricklefs 1993, Bakken *et al.* 2002, Ricklefs & Williams 2003), certain weather events influence the potential feeding habitats of coastal birds in the Wadden Sea. Responses of reproducing birds to such weather-induced variation in food resources can be relatively simply predicted in specialist feeders such as Common Tern, Oystercatcher and Avocet (see, for example, Becker & Specht 1991). However, it has never been observed how breeding opportunists may respond to weather events given above, how weather may affect reproduction of these birds and what the quantitative effects on reproductive output may be.

The Black-headed Gull is an opportunistic feeder potentially foraging on marine as well as terrestrial prey (Götmark 1984, Gorke 1990, Kubetzki & Garthe 2003). The results found in this species suggest that rain, wind and temperature have varying effects during different stages of breeding performance. Clutches laid during rainy periods were bigger than those laid during dry periods and frequent rain increased probability of chick survival until fledging. Rain during the laying phase and the phase of linear growth reduced egg and chick predation, respectively. Thus, rain had basically positive effects on reproductive output, though, if occurring during the early postnatal phase, it caused retarded chick growth and low fledging mass. Low temperature during the laying phase affected egg predation positively, but had no effects on the life-history traits studied, i.e. egg size, clutch size and parameters of chick development. In addition, storms during egg laying had negative effects on clutch size but storms during the phase of asymptotic growth increased fledging success and reduced chick predation. Most of these weather-related phenomena should indeed be explainable by effects of weather on the food supply used by the gulls during egg production and chick provisioning. Since rain and relatively high temperatures are assumed to positively affect availability of benthic and terrestrial food (see above), birds should respond to such conditions by allocating resources to bigger clutches (e.g., Kitaysky *et al.* 2000) and to more intensive parental care including chick provisioning and time allocated to nest and brood attendance to reduce predation (e.g., Oro *et al.* 1997, Gill *et al.* 2002). Owing to its negative effects on potential food, wind should have converse effects on reproductive traits and chick survival. Positive effects of wind occurring prior to fledging on pre-fledging survival may be explicable by kleptoparasitism of the gulls on co-existing Common Terns increasing with wind speed (cf. Gorke 1990, Stienen *et al.* 2001).

In this respect, the results obtained from Black-headed Gulls during the 1990s fit very well in relatively well known mechanisms of weather on coastal bird reproduction. However, they furthermore give some interesting insights into breeding ecology of gull species breeding in the Wadden Sea which may have implications for the breeding range expansion of Black-headed Gulls during the past century. Gorke (1990) suggests that availability of terrestrial prey may depend to a greater extent on rain than intertidal prey. Considering this assumption, the positive effects of rain as given above could indicate an at least supplemental usage of coastal grassland located adjacent to the colony studied. Being arguably a more consistent and more predictable food supply, this supplemental usage could ultimately even be responsible for the low interannual variability in Black-headed Gull reproduction. Chick development and breeding success were remarkably constant during the 1994-1997 period with the exception of 1996 (see Table 2.2). Retarded chick growth and slightly lower breeding success in 1996 may be explainable by the exceptionally low precipitation during June 1996 (see Fig. 2.2). Additionally, that breeding season succeeded a severe winter which had lasting negative effects on benthic food supply (Armonies *et al.* 2001). The ability of Black-headed Gulls to switch between independently existing food supplies with positive consequences for level and variability of breeding success could possibly play an important role in breeding range expansion and a successful establishment of a large Wadden Sea breeding population.

1.8. Effects of habitat selection on coastal bird reproduction

The selection of an appropriate breeding habitat supplying convenient food availability and including a nest-site safe from predation, weather and flooding is among the most important preparations facilitating a successful breeding attempt (see sections above). Given that these conditions vary among different patches of an ecosystem or a biotope, breeding densities should vary in accordance with habitat attractiveness. Given, moreover, that birds assess proximate cues correctly during breeding habitat and nest-site selection, higher hatching success and breeding success should be predicted for habitats with highest breeding densities. Besides nest-site selection, birds evolved several antipredator behavioural mechanisms to avoid or minimise predation of offspring. Owing to a “dilution effect”, colonial breeding including an effective communal mobbing behaviour is presumed to be advantageous for each individual clutch or brood (Wittenberger & Hunt 1985, Furness & Monaghan 1987). Other strategies of antipredator behavioural patterns include effective aggressive responses against predators (e.g., Kis *et al.* 2000, Ostreiher 2003) or predator avoidance by building well concealed nests (e.g., Conway & Martin 2000, Weidinger 2002, Bennett & Owens 2002). These specific behavioural capabilities should be reflected in the requirements on breeding habitat and nest-site.

Among the species addressed in this study, the Redshank is the only one which breeds non-colonially (like Oystercatchers), and which has to rely on concealing its clutch in vegetation to protect it passively from predation (in contrast to Oystercatchers). Although effects of vegetation on reproduction have been shown even in open-nesting waders and gulls (Reid *et al.* 2002, Kim & Monaghan 2005), Redshank habitat and nest-site selection should be more linked to topographic and vegetational habitat characteristics than that of any other species studied. As shown, for example by Ens *et al.* (1992) and Heg (1999), breeding density as well as reproductive output of Oystercatchers is higher in territories adjacent to tidal flats (resident territories) than in those remote from the flats (leapfrog territories) reflecting the advantage of unrestricted access to foraging territories. Assuming that access to tidal flats should also be an ultimate cue in Redshanks, birds should have to trade off during habitat and nest-site selection between breeding next to tidal flat foraging territories and breeding concealed and safe from egg predators in more productive and well structured vegetation of late succession stages, which are normally located away from the shoreline (Ellenberg 1996). These topics were studied in Redshanks applying approaches of different spatial scales, i.e. on the scale of habitat (see section 3.) and nest-site (see section 4.). In 1994, the birds bred with higher densities and slightly higher hatching success in a well structured habitat dominated by orthotropic herbs (*Atriplicetum littoralis*) than in habitats dominated by different grass species (*Puccinellietum maritimae, Agropyretum repentis*). Since the preferred habitat coincided with proximity to shoreline and tidal flats, respectively, the ultimate cues (food supply or predator avoidance) of habitat selection and the causes of positive reproductive consequences could not be defined by this study. The second, more detailed approach revealed an absence of effects of distance to shoreline on hatching success but rather positive relationships between hatching success and chronosequence, vegetation structure and nest concealment. However, these relationships were not directly causal ones but rather appeared to interact with timing of breeding: early breeding led to successful incubation possibly owing to temporal avoidance of highest predation pressure (cf. Götmark 2002). Early breeding was in turn largely facilitated by concealed nest-sites supplied in *Festuca rubra* and *Elymus repens* communities (cf. Esselink 2000). These results suggest that Redshanks, in contrast to Oystercatchers, should indeed benefit from selecting habitats characterised by vegetation of advanced chronosequence and succession at least in terms of hatching success, but possibly even in terms of reproductive output. At least in a predator rich environment such as the study site at the Jadebusen, Redshank habitat and nest-site selection in saltmarshes should be constrained by predation rather than by tidal flat food supply, in contrast to Oystercatchers.

These results have even several implications for management of saltmarshes and saltmarsh breeding birds. As discussed, for example, in section 3., managing saltmarshes by mowing or cattle grazing even on a relatively low level should be disadvantageous for abundance as well as for reproductive success of Redshanks (cf. Norris *et al.* 1997, 1998, Thyen 2000). As confirmed by the results above, Redshank hatching success should indeed be higher in saltmarshes with relatively undisturbed development and vegetation. Factors affecting seasonal and successive development of saltmarshes, such as agricultural usage (Bakker 1985, 1990, Thyen 1996b), clay removal (Flemming 2003) or sea-level rise (Smart & Gill 2003, Hughes 2004), could potentially impair Redshank reproduction at least, at sites with high predation pressure.

1.9. Implications for monitoring breeding success of coastal birds

The most fundamental results of the presented analyses are that reproductive traits and reproduction itself are subject to a high spatial variability within the Wadden Sea ecosystem, and in some species even to a high short-term temporal variability. The population trends of some species being constant or even increasing on a large scale should partly be only explained by small-scale migration processes among breeding sites, as presumably in Redshanks and Oystercatchers. Further important results include the fact that the impact of influencing factors varies among breeding sites and, possibly even more importantly, among species representing different life-histories and ecologies. Different species should therefore be differentially susceptible to environmental conditions and changes in food supply and habitat, for example. All of these topics have several implications for monitoring breeding success and further demographic parameters in coastal bird populations.

As stressed by several authors, integrated population monitoring should be an essential tool in species conservation (e.g., Baillie 1990, 2001 Hötker 1999, Bairlein *et al.* 2000). By recording population size, productivity, recruitment and survival rate, demographic causes of population changes can be determined and to some extent even be localised and qualified. Integrated population monitoring has, thus, the potential to serve as instrument in species as well as habitat and ecosystem conservation. For coastal birds breeding in the Wadden Sea, respective data are unfortunately only available for a very limited number of species (see above) and are currently completely lacking for very abundant wader and gull species, such as Redshanks and Black-headed Gulls. This is a considerable lack since many species experienced a spectacular population development during recent decades which mostly is not coherently explainable due to the lack of data on mortality rates and breeding success. In the two species mentioned, population trends considerably vary between different regions of their breeding range making it indispensable, in terms of species and ecosystem conservation, to model spatial and temporal population dynamics based on demographic monitoring data.

Besides monitoring demography including breeding success to explain and predict population changes, individual coastal birds and their reproductive traits can be used as indicators reflecting environmental conditions and changes within an ecosystem (Furness & Greenwood 1993, Becker 2003). As particularly shown in Black-headed Gulls (see section 2.), reproductive traits such as clutch size and chick developmental parameters vary by weather parameters and, ultimately, by foraging conditions qualifying these traits as sensitive indicators of respective influencing factors affecting even hatching and breeding success (Walsh *et al.* 1991, De Boer & Koks 1997, Becker *et al.* 1997a). The same should be true for further factors (e.g., environmental contamination; see Munoz Cifuentes 2004) and for further indicator species being representative for different compartments of the ecosystem according to their specific habitats and foraging sites.

The intrinsic value of coastal birds as well as its value as sensitive indicators for a variety of biological and chemical parameters (see section 5.) were acknowledged by the *Trilateral Wadden Sea Co-operation* by initiating the *Trilateral Monitoring and Assessment Program* (TMAP) including a wide set of defined issues of concern, ecological targets and monitoring parameters (Bakker *et al.* 1997, Trilateral Monitoring and Assessment Group 2000, Marencic & Lüerßen 2001). With respect to breeding coastal birds, numbers and distribution, breeding success, and egg contamination are suggested to be monitored to ensure a "natural breeding success" and to assess responses of breeding birds to pollution levels and to recreational activities (Trilateral Monitoring and Assessment Group 2000). This set of monitoring parameters, i.e. population size, breeding success and egg contamination, could ideally be applied as a kind of "early warning system": Current population size records could be sufficient to predict future population changes derived from annual reproductive output and to identify and quickly anticipate negative environmental impacts on populations (Becker 1991, Thyen *et al.* 2000, Becker 2003). However, apart from a two year pilot study conducted in the breeding season 1996 and 1997 (section 5.), and a few short-term and single species approaches (De Boer & Koks 1997, Stienen *et al.* 1998), the parameter "breeding success" is currently not implemented within the TMAP.

Regardless that "natural breeding success" as an ecological target can only be ensured by determining "natural background values" of reproductive output in the long-term, at representative breeding sites and in several species, this study provides strong evidence to the necessity of monitoring breeding success. As shown in Redshanks, for example, a stable breeding population does not inevitably represent largely favourable breeding conditions. Low reproduction in apparently stable coastal bird populations cannot be excluded, at least in regionally and temporarily restricted hot spots. To recognise these phenomena and to react with suitable counter-measures prior to population declines, an integrated approach to population monitoring of coastal birds and their reproduction is a necessity. It therefore has to be urgently recommended to implement the parameter "breeding success" within the TMAP including a long-term time frame for several breeding sites of different attractiveness and reproductive quality throughout the international Wadden Sea and several species with different life-histories and ecologies. Although relatively intricate, the spectrum of indicator species investigated in the pilot studies should be extended to the Redshank being the only coastal bird species representing concealed breeding and, thus, a monitor of saltmarsh suitability for breeding birds concerning its vegetation, structure and predator community.

2. Effects of Individual Life-history Traits and Weather on Reproductive Output of Black-headed Gulls *Larus ridibundus* Breeding in the Wadden Sea, 1991 - 1997

Stefan Thyen and Peter H. Becker

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Abstract

Capsule Annual breeding success was relatively constant and is shown to be related to clutch size and growth rate and to be positively affected by rain during egg-laying and advanced chick rearing phase.

Aims To provide the first-time long-term data on breeding success of Black-headed Gulls in the Wadden Sea, to analyse its intrinsic and environmental covariates, and to re-assess the significance of the ice-winter 1995/1996 on reproduction.

Methods In a relatively small colony at the Wadden Sea coast, clutches were selected randomly and enclosed to determine clutch size, egg biometrics, hatching and breeding success, and chick development in 1991 and from 1994 to 1997. Weather data (temperature, rain, wind) were related to life-history traits (clutch size, egg volume, chick development) and reproductive success.

Results Mean annual breeding success was 0.7 fledglings per pair. In 1996, breeding success tended to be lower and chick growth rate was significantly lower. Hatching success was lower in small clutches, chick mortality increased with decreasing chick growth rate. Rain during the egg laying phase increased clutch size and decreased clutch predation. Rain during the early postnatal phase impaired chick growth. Rain during the phase of linear growth affected chick growth and fledging success positively and brood predation negatively.

Conclusions Breeding success of Black-headed Gulls breeding in the Wadden Sea is relatively constant between years probably due to the use of terrestrial and marine feeding habitats. Rain most likely increases the availability of intertidal and terrestrial prey and, thus, affects time-budgets and food provisioning of parents positively. Lower breeding success in 1996 might have been caused by a relatively dry breeding season and possibly even by a preceding ice-winter.

2.1. Introduction

Individual life-history traits in birds such as timing of breeding, egg, clutch and brood size are related to reproductive output in a complex framework. Traits are more or less variable due to parental quality and decisions aimed to maximise lifetime reproductive success and induced by intrinsic factors (e.g., age, experience, condition) as well as variability of environmental conditions (Klomp 1970, Clutton-Brock 1991, Stearns 1992, Wendeln & Becker 1999). For example, food supply has been shown several times to affect breeding performance and success of seabirds by affecting parental condition (Frank & Becker 1992, Monaghan *et al.* 1992), timing of breeding (Ratcliffe *et al.* 1998, Regehr & Rodway 1999), egg size (Croxall *et al.* 1992), clutch size (Ratcliffe *et al.* 1998) and chick mortality (Gill *et al.* 2002, Oro & Furness 2002). Food availability is frequently related to weather. In piscivorous seabirds, for example, rain and wind can impair foraging and food provisioning (Becker &

Specht 1991, Frank 1992, Finney *et al.* 1999, Stienen *et al.* 2000). Thus, weather can affect breeding success of birds indirectly by affecting food availability and directly by affecting chick development and mortality mainly of relatively young nestlings (Becker & Finck 1985, Becker & Specht 1991).

To use these interrelationships as conceptual basis for monitoring projects and population models, a proper knowledge of specific breeding success and its environmental covariates of the addressed species is needed (Furness & Greenwood 1993, Thyen *et al.* 1998). Such information is completely lacking for Black-headed Gulls (*Larus ridibundus*) breeding in the Wadden Sea. In this species, a northwards breeding range expansion has been taking place since the end of the nineteenth century including the settlement of the German North Sea coast in the 1930's (Vauk & Prüter 1987, Hagemeijer & Blair 1997). Presently, the Black-headed Gull is the by far most abundant breeding bird species of the Wadden Sea whose population is still growing (Garthe *et al.* 2000). Foraging ecology of Wadden Sea colonies was studied several times (e.g., Gorke 1990, Kubetzki & Garthe 2003). However, no studies on breeding were conducted to explain and model the rapid development mentioned above. Breeding success of Black-headed Gulls was firstly studied during a two-year project on breeding success of several coastal bird species breeding in the Wadden Sea (Thyen *et al.* 1998). Low breeding success and retarded chick growth were found in 1996 compared to 1997. These findings were attributed to a potentially reduced benthic food supply due to an ice-winter preceding the 1996 breeding season. That winter was characterised by an above-average duration of coastal ice-drift and tidal flat ice cover followed by a decline of some macrobenthos species (Klaus Strübing pers. comm., Armonies *et al.* 2001). However, the assumption of negative effects of the extreme winter could not be confirmed owing to the lack of comparative studies on effects of weather and food supply on breeding success of Black-headed Gulls.

Here, long-term data on Black-headed Gull breeding biology were analysed using data collected between 1991-1997 in a small mainland colony at the German Wadden Sea coast. We aim to provide long-term data on breeding success and chick development of the currently most abundant breeding bird species of the Wadden Sea for the first time. We furthermore aim to investigate effects of weather and its interactive effects with life-history traits on breeding success, and to re-assess the potential effects of the ice-winter 1995/1996 on the succeeding breeding season.

2.2. Methods

2.2.1. Study area and weather

The study area is located within the National Park "Niedersächsisches Wattenmeer", Germany. Black-headed Gulls bred on the mainland in the lower salt marshes of the north-eastern Jadebusen (N 53°31', E 8°18'; Fig. 2.1). The colony site was located adjacent to grassland and arable land. During the study years, the colony size varied between about 150 (1991) and 300 (1994/1995) pairs. Breeding started usually at the end of April and ended at the beginning of July. Marsh Harriers *Circus aeruginosus*, Oystercatchers *Haematopus ostralegus*, Herring Gulls *Larus argentatus*, Red Foxes *Vulpes vulpes* and mustelids occurred as potential egg and chick predators.

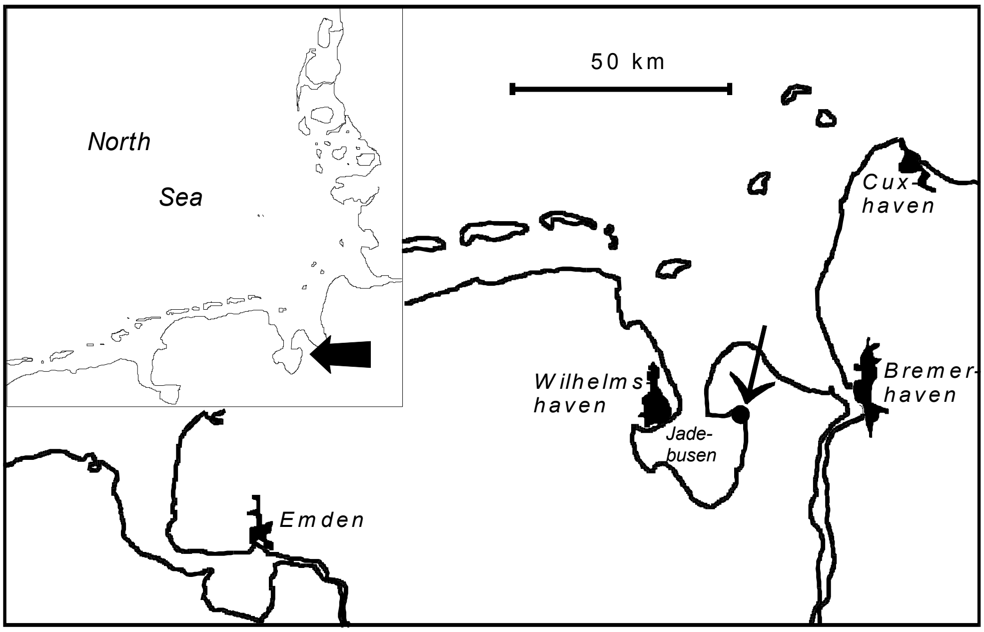

Fig. 2.1: Location of the Black-headed Gull colony site studied at the German North Sea coast.

According to data of the “Deutscher Wetterdienst” recorded in Wilhelmshaven, Germany, the weather of most breeding seasons studied was not significantly different from long-term means measured 1969-1998 (Fig. 2.2). However, weather during the seasons 1991 and 1996 deviated from long-term means in some parameters. Temperature in May and June, respectively, was slightly below average. Precipitation in June 1991 was far above, that in June 1996 far below the long-term mean.

2.2.2. Recording of breeding parameters

Recording of reproductive parameters was performed according to methods given by Thyen *et al.* (1998). In 1991 and from 1994 to 1997, clutches were randomly selected from the beginning of May and subsequently inspected at regular intervals (2 ± 1 days) to record the fate of eggs and chicks. At clutch finding, clutch size was recorded and egg length and breadth were measured using a calliper (precision ± 1 mm). The date of egg laying was determined to the nearest pentad (five day periods of the year) leading to an estimation of the expected hatching date. About two weeks after clutch registration, nests were enclosed to permit regular recording of chick mass and fate. This method is proved to be well applicable in several larid species including the Black-headed Gull (Viksne & Janaus 1980, Thyen *et al.* 1998; but see Jehl 2001). Chicks were banded directly after hatching to assign them to clutches and eggs, respectively. Chicks were regularly weighed using an electronic balance (precision ± 0.1 g) within a wind-proof box (Wagener 1998). Measuring intervals were mostly two days, but intervals varied occasionally due to adverse weather.

During each inspection, dates and causes of egg and chick losses were recorded. Eggs as well as chicks were classified as being depredated if they were lost before the assumed hatching and fledging date, respectively. An incubation duration of 24 days was assumed (Glutz von Blotzheim & Bauer 1999). Chicks were able to leave the enclosures at an age of about three weeks. All chicks that disappeared after 21 days were classified as being fledged

(Thyen *et al.* 1998). Because of unreliability of defining predators from nest remains (Larivière 1999) and since most eggs and chicks disappeared without a trace, predator species were not determined. Clutches were classified as being deserted if eggs were found cold and damp at successive inspections. Causes of desertion could not be determined. Losses due to flooding could easily be recognised by definite traces such as mud and driftline material within the nesting territory. Additionally, dead chicks without external injuries were found frequently during colony inspections. These chicks were classified as losses due to undefined “intrinsic causes” (starvation, hypothermia, diseases, etc.).

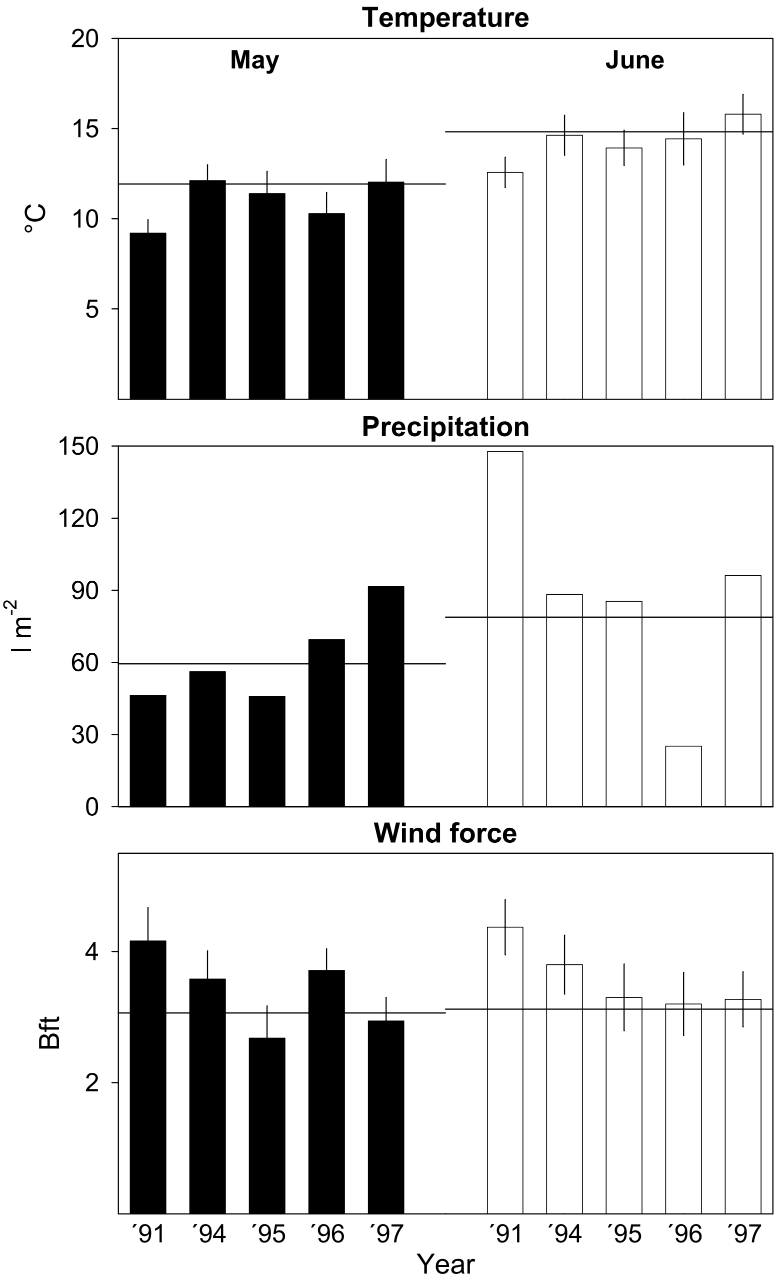

Fig. 2.2: Weather during May (black bars) and June in the study years as measured by Deutscher Wetterdienst in Wilhelmshaven. Mean daily averages ± 95% confidence intervals of temperature, sum of precipitation, mean daily maximum wind force ± 95% confidence intervals and long-term means 1969-1998 (horizontal lines) are given.

2.2.3. Data analysis

Clutch size, egg volume index and chick growth parameters were regarded as life-history traits potentially affected by weather and affecting reproduction by interacting or covarying with weather parameters. Egg volume index was calculated by egg length * breadth^2 * 0.001 (Becker & Erdelen 1986). To describe the growth of chicks, growth curves were generated. Data on chick masses were fitted to a cubic rather than to a logistic model to account for the mass recession prior to fledging, which is typical for many larid species. Hatching mass and growth rate of chicks were calculated as given by Thyen *et al.* (1998). Hatching mass is defined as body mass of chicks of an age of one or two days (see above). Growth rate was calculated as mean daily increase in body mass during the phase of linear growth which itself is defined as period from 5 to 15 days after hatching.

Effects of weather on reproduction were analysed by examining effects of intensity and duration of particular weather phenomena during different stages of Black-headed Gull breeding performance. Weather data were recorded by the “Deutscher Wetterdienst” in Wilhelmshaven at a distance of about 14 km from the colony site. The relatively sheltered position of this station within a bay (Jadebusen) is comparable to that of the colony site. Consequently, trends and variations of weather data are directly transferable to the colony. Mean daily average temperature (average calculated from daily minimum and maximum temperature in °C), mean daily maximum wind force (Bft), sum of precipitation (l * m^{-2}) and number of rainy ($\gtrsim$ 1 l * m^{-2}) and stormy days ($\gtrsim$ 6 Bft) were calculated for each pentad of a year. Weather data were then related to different breeding phases of each breeding pair. Incubation periods were subdivided into laying phase (including pentad of egg-laying and two pentads prior to laying) and incubation phase (including pentad of egg-laying and four succeeding pentads). Pre-fledging periods were subdivided into postnatal phase (including the pentad of hatching), phase of linear growth (including two pentads succeeding the postnatal phase) and phase of asymptotic growth (including two pentads succeeding the linear growth phase).

Clutches were sampled at random (see above). However, in 1991 a random clutch sample was studied on size, egg biometrics and hatching success but only 3-egg clutches were enclosed and examined on chick development and breeding success. To avoid biases in analysing variations by year and effects of weather on clutch and egg size, the 1991 sample was excluded from respective analyses. Additionally, one egg per clutch was randomly sampled and removed from selected 3-egg clutches in 1991 (21 % of clutches sampled totally), 1995 (48 %) and 1996 (38 %) for analysing pollutant concentrations (see Munoz Cifuentes 2004). In these clutches, relative hatching success and frequency of chick losses were calculated on the basis of the artificially reduced egg numbers.

2.2.4. Statistics

Statistics were performed according to Jongmann *et al.* (1995) and Sachs (1997) applying SPSS 10.0 statistical package. All tests were two-tailed. In most analyses, multivariate statistics were applied to reveal weather effects on life-history traits and to analyse effects of life-history traits and weather on hatching success, fledging success and chick development. In all cases, predictor variables were entered forward stepwise into the analyses.

Table 2.1: List of variables entered into the logistic regression models applied in this study. LP = laying phase, IP = incubation phase, PP = postnatal phase, LGP = phase of linear growth, AGP = phase of asymptotic growth (see text for definitions). “Intrinsic mortality” includes mortality caused by starvation, hypothermia, etc.

Variables	LP	IP	PP	LGP	AGP
Dependent					
Hatching	X	X			
Clutch predation	X	X			
Fledging			X	X	X
Brood predation			X	X	X
Intrinsic mortality			X	X	X
Independent					
Weather parameters	X	X	X	X	X
Clutch size	X				
Egg volume index	X				
Hatching mass			X		
Linear growth rate			X	X	
Clutch size * weather parameters	X				
Egg volume * weather parameters	X				
Hatching mass * weather parameters			X		
Growth rate * weather parameters			X	X	

To test variation in clutch size under different weather conditions during associated laying phases (see above), weather variables were grouped in two classes discriminated by long-term (1969-1998) arithmetic means above and below average. Differences in clutch size were consecutively tested using non-parametric tests. In all other cases, weather effects were tested in multiple linear regression analyses in the case of continuous dependent variables (egg volume index, parameters of chick development) and in multiple logistic regression analyses in the case of dichotomous dependent variables (hatching of eggs, fledging of chicks, predation of eggs and chicks, intrinsic mortality of chicks). Multiple analyses of weather effects were separately conducted for different stages of incubation and chick development, respectively (Table 2.1). Parameters of life-history traits were included in the logistic regression models as relevant for the respective breeding stage. To discriminate between direct effects of the traits on hatching, fledging and mortality and those interacting with weather parameters, main effects as well as two-way interactions were analysed.

2.3. Results

2.3.1. Annual variation in reproductive parameters

Most reproductive parameters analysed did not vary significantly between years although clutch size, egg volume, hatching and breeding success appeared to be comparatively low in

Table 2.2: Parameters of Black-headed Gull breeding biology from Augustgroden 1991 – 1997. Given are means ± sd and percentages (relative hatching and breeding success). P according to K-W-tests ^{a}, χ^2-tests ^{b}, and ANOVA ^{c}. Note that in 1991, 1995, and 1996 eggs were randomly removed from clutches to analyse pollutant concentrations in eggs (see methods for details). In 1991, only three-egg clutches were investigated for breeding success and chick development. Respective data were excluded from analyses.

	1991	1994	1995	1996	1997	*P*	total
n clutches	62	16	25	16	18		137
clutch size	2.5 ± 0.8	2.8 ± 0.5	2.5 ± 0.8	2.4 ± 0.7	2.7 ± 0.6	0.690 ^{a}	2.6 ± 0.7
egg volume index	71.4 ± 6.2	72.4 ± 5.5	72.0 ± 6.3	69.8 ± 4.8	71.9 ± 5.0	0.281 ^{c}	71.4 ± 6.6
hatching success							
n chicks	94	23	34	19	35		205
chicks * clutch $^{-1}$	1.6 ± 1.1	1.4 ± 0.7	1.2 ± 1.3	1.2 ± 1.1	1.9 ± 1.2	0.328 ^{a}	1.5 ± 1.1
% of eggs	71.8	52.3	68.6	57.6	71.4	0.336 ^{b}	64.2
breeding success							
n fledglings	–	12	20	6	14		95
fledglings * clutch $^{-1}$	–	0.8 ± 0.9	0.8 ± 1.1	0.6 ± 1.1	0.8 ± 1.0	0.918 ^{a}	0.7 ± 1.0
% of chicks	–	52.2	58.8	31.2	40.0	0.199 ^{b}	53.4
chick development							
hatching mass [g]	–	26.9 ± 3.0	31.0 ± 7.1	25.7 ± 7.2	29.3 ± 4.8	0.003 ^{c}	29.1 ± 5.9
growth rate [g/d]	–	12.5 ± 2.7	12.4 ± 3.5	7.5 ± 2.4	13.1 ± 1.6	0.001 ^{c}	11.7 ± 3.1
fledging mass [g]	–	264.6 ± 30.9	258.4 ± 21.3	240.5 ± 16.0	251.6 ± 24.6	0.218 ^{c}	253.4 ± 24.7

1996 (Table 2.2). In contrast, significant differences were found in hatching mass (ANOVA: $F_{3,\,91} = 5.117$, $P = 0.003$) and growth rate (ANOVA: $F_{3,\,74} = 5.712$, $P = 0.001$; Fig. 2.3). As revealed by Scheffé-tests, average hatching mass was lower in 1996 ($n = 9$) than in 1995 ($n = 34$) and 1997 ($n = 33$; $P = 0.006$ and 0.029, respectively) and mean growth rate was lower in 1996 ($n = 7$) than in all other years (1994: $n = 16$, $P = 0.012$; 1995: $n = 28$, $P = 0.008$; 1997: $n = 23$, $P = 0.002$; 1991 excluded from analyses).

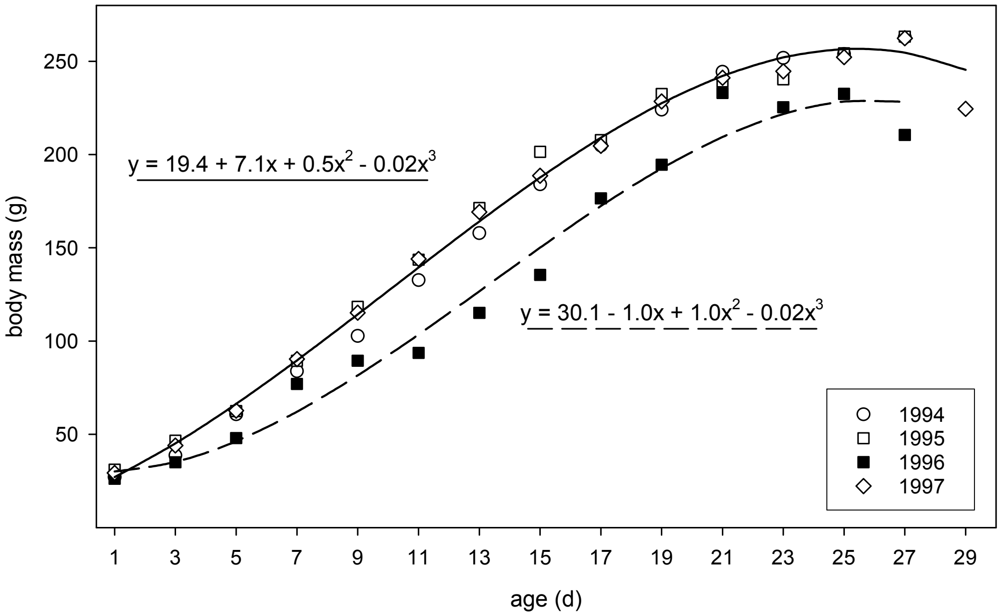

Fig. 2.3: Development of Black-headed Gull chicks hatched in 1994, ´95, and ´97 (open symbols, solid line) compared to that of chicks hatched in 1996 (filled symbols, dashed line). Mean body masses per age group and curves fitted by cubic models are presented. Curve fittings are based on single values of body masses rather than on the means presented. Solid line: $R^2 = 0.942$, $F = 3942.45$, $n = 731$, $P < 0.001$; dashed line: $R^2 = 0.894$, $F = 216.84$, $n = 78$, $P < 0.001$.

2.3.2. Causes of egg and chick losses

The most frequent causes of offspring losses were predation and colony flooding. Furthermore, a relatively high share of chicks was found dead without external injuries. Frequencies of egg ($\chi^2_{12} = 65.702$, $P < 0.001$) and chick losses ($\chi^2_{9} = 25.908$, $P = 0.002$; 1991 excluded from analyses) varied considerably between years. In 1994 and 1995, predation of chicks was relatively low (Fig. 2.4). In 1996, egg as well as chick predation was high. In 1997, no eggs, but a high share of chicks, were predated. Floods led to relative high losses of offspring especially in 1994, 1996 and 1997. Chicks found dead for no apparent external reason occurred in all study years but relatively less frequent in 1997.

2.3.3. Effects of weather on egg and clutch size

Mean clutch size varied by several weather parameters. Clutches laid during periods characterised by levels of precipitation above average were larger than those laid at relatively dry periods (2.7 ± 0.6, $n = 71$ vs. 2.4 ± 0.8, $n = 62$; U-test: $U = 1805.5$, $P = 0.025$), and clutches laid during periods with frequencies of rainy days above average were larger than those laid during periods with number of rainy days below average (2.7 ± 0.7, $n = 77$ vs.

2.4 ± 0.8, *n* = 56; *U* = 1705.0, *P* = 0.01). In contrast, storms had negative effects on clutch size: Those laid during periods with frequencies of stormy days above average were smaller than those laid at less stormy periods (1.8 ± 0.9, *n* = 12 vs. 2.7 ± 0.6, *n* = 121; *U* = 372.0, *P* < 0.001). No further clutch size variation due to weather parameters was found. In addition, no relationships were found between weather parameters and average egg volumes * clutch^{-1} (multiple linear regression analyses).

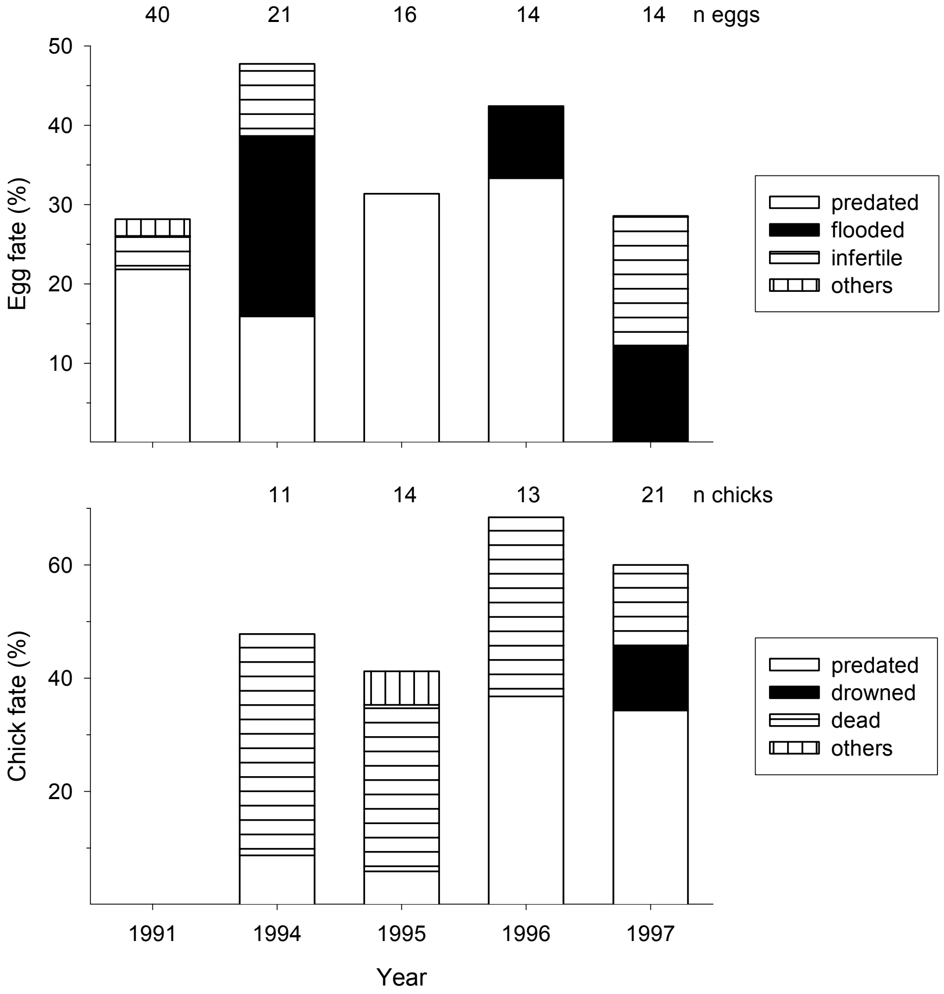

Fig. 2.4: Egg (upper graph) and pre-fledging chick mortaliy of Black-headed Gulls 1991-1997. Data on chick mortality from 1991 are excluded from analyses (see methods).

2.3.4. Factors affecting hatching success and clutch predation

As predicted by a multiple logit regression analysis (χ^2 = 21.57, df = 1, *P* < 0.001, R^2 = 0.24, *n* = 133 clutches), hatching of clutches was positively related to clutch size (*B* ± se = 1.33 ± 0.3, *P* < 0.001) but not to egg volume, weather during the egg laying period and interactions among life-history traits and weather parameters. Relative hatching success was lower in one- (33.3 %) than in two-egg (66.7 %) and three-egg clutches (68.8 %). A further multiple analysis revealed negative effects of temperature during the phase of egg laying (*B* ± se = -0.31 ± 0.14, *P* = 0.03) and of clutch size interacting with precipitation during egg laying (*B* ± se = -0.02 ± 0.01, *P* < 0.001) on clutch predation. In contrast, hatching and predation of clutches were not affected by weather during the period of incubation.

2.3.5. Effects of weather on chick development

Multiple linear regression analyses revealed significant relationships between weather parameters and chick growth parameters only for the postnatal phase, but not for the phases of linear and asymptotic growth (n = 84 broods). Number of rainy days during the postnatal phase was negatively related to linear growth rate (B ± se = -0.62 ± 0.29, P = 0.036; model statistics: F = 4.56, df = 1, P = 0.036, R^2 = 0.06). Additionally, analyses predicted a negative effect of height of precipitation on fledging mass (B ± se = -0.80 ± 0.38, P = 0.036; model statistics: F = 4.45, df = 1, P = 0.040, R^2 = 0.08).

Table 2.3: Results of stepwise multiple logistic regression analyses examining the effects of life-history traits and weather on fledging and mortality of Black-headed Gull broods during different stages of chick development. Only significant relationships are presented. For the whole set of variables included into the models see Table 2.1. Besides regression coefficients, model statistics are given. n = 84 broods were included in each analysis. See methods for definitions of parameters and phases. HM = hatching mass, NRD = number of rainy days, LGR = linear growth rate, TEM = temperature, WIF = wind force.

	Fledging		Brood predation		Intrinsic mortality	
	$B \pm$ se	P	$B \pm$ se	P	$B \pm$ se	P
postnatal phase	χ^2 = 5.66, df = 1, P = 0.017, R^2 = 0.10		no variable included		no variable included	
HM * NRD	0.02 ± 0.01	0.023				
Linear growth	χ^2 = 11.23, df = 2, P = 0.004, R^2 = 0.21		χ^2 = 6.59, df = 1, P = 0.010, R^2 = 0.13		χ^2 = 9.91, df = 1, P = 0.002, R^2 = 0.18	
NRD	0.33 ± 0.16	0.039	-0.38 ± 0.15	0.014		
LGR * TEM	0.02 ± 0.01	0.007			-0.02 ± 0.01	0.004
asymptotic growth	χ^2 = 14.08, df = 2, P = 0.001, R^2 = 0.21		χ^2 = 8.65, df = 1, P = 0.003, R^2 = 0.15		no variable included	
NRD	0.33 ± 0.12	0.008				
WIF	2.19 ± 0.77	0.005	-2.28 ± 0.82	0.006		

2.3.6. Factors affecting fledging and chick mortality

Fledging and mortality of chicks was affected by chick development and weather during different stages of chick development (Table 2.3). Fledging of chicks was positively affected by duration of rain during all growth phases and by hatching mass and linear growth rate interacting with duration of rain and temperature, respectively. Wind speed during the phase of asymptotic growth had an additional positive effect on fledging. In contrast, brood predation decreased with increasing duration of rain during linear growth and with increasing wind speed during asymptotic growth. Intrinsic mortality of chicks was negatively related to linear growth rate interacting with temperature.

2.4. Discussion

The results suggest that variability of individual life-history traits (clutch size, growth rate), weather and covariations between respective parameters affect breeding in Black-headed Gulls in the Wadden Sea. Specifically, rain affected breeding success mainly by increasing clutch size and decreasing clutch predation and by increasing pre-fledging chick survival. The significance of the ice-winter preceding the 1996 breeding season on (not significantly) lower reproduction and retarded chick growth cannot be completely explained by the results. The relative dryness of this season may have had at least an additional effect on reproduction of the Black-headed Gulls.

Clutch size is apparently a parameter of fundamental importance in Black-headed Gull reproduction: Hatchability varied by clutch size. Rain and wind during the phase of egg-laying affected clutch size and predation of eggs. As predicted by life-history theory, specific clutch size evolves from the ability of parents to raise a particular number of chicks at least in nidiculous species. However, clutch size is intraspecifically variable within certain limits in many bird species. It depends on parental decisions aimed to maximise lifetime reproductive success (Lack 1947, Stearns 1992). Especially in unfavourable environments and under temporarily unfavourable conditions such as food shortage or reduced food availability, breeding birds have to trade-off between investing in current reproduction or in their “residual reproductive value” by decreasing costs of reproduction or abstaining from reproduction and, thus, by maintaining or increasing body condition. As shown in several species, birds frequently are constrained to adjust clutch size and/or egg size or even to refrain from egg laying when food availability is reduced (e.g., Becker *et al.* 1985, Ratcliffe *et al.* 1998, Kitaysky *et al.* 2000). In our study, no significant variation in egg volume could be proved. Variability of clutch size, however, can probably be explained by foraging constraints as suggested by the effects of weather on clutch size: Black-headed Gull adults as well as chicks preferably forage on lumbricids and insects in inland habitats. In marine habitats, prey taken during low tide (e.g. polychaets such as *Hediste diversicolor* and molluscs such as *Hydrobia ulvae*) is important but terrestrial food is supplemented when available within the foraging range (Gorke 1990, Kubetzki & Garthe 2003). Surface activity of terrestrial and intertidal prey is positively affected by substrate moisture and temperature. Availability, especially of terrestrial prey but possibly also of intertidal organisms for visual predators such as Black-headed Gulls, consequently should be positively affected by temperature and rain and negatively by wind (see Pienkowski 1983a, Edwards & Bohlen 1996) resulting in relatively large clutches during relatively wet and less windy egg-laying periods. These effects of weather on food availability could also be responsible for the negative effects of temperature and rain on egg predation. Reduced food supply constrains breeding birds frequently to increase foraging effort and to inevitably reduce time available for nest attendance and anti-predator behaviour (e.g., Oro *et al.* 1997, Caldow & Furness 2000, Gill *et al.* 2002). Similarly, unfavourable weather conditions during the egg-laying phase as described above could constrain Black-headed Gulls not only to reduce “reproductive potential” by producing smaller clutches but to accept additionally higher egg predation and lower hatching success due to time budget alterations.

Similar to clutch size and egg mortality, chick development, mortality and fledging were affected by rain, wind and temperature during several stages of the pre-fledging period. Frequency of rain during the postnatal phase caused growth retardation of chicks and even reduced fledging mass. Growth rates interacting with temperature were negatively related to “intrinsic mortality” suggesting that starvation and hypothermia were likely the most important intrinisic causes of mortality. Rain during phases of linear and asymptotic growth affected fledging of chicks positively and predation negatively. The latter confirmes that rain should have positively affected food availability (see above). However, effects of rain on chick development and survival obviously change its signs during the pre-fledging period. These changing effects probably reflect progressing physiological development of chicks on one hand, and adjusted responses of parents to chick requirements and environmental conditions on the other hand. As with most other bird species, young Black-headed Gull chicks should be vulnerable to temperature, rain and wind due to the lack of independent thermoregulation (Starck & Ricklefs 1998). This fact could lead to a parental trade-off between brooding and food provisioning (e.g., Becker & Finck 1985, Beintema & Visser 1989a, Becker & Specht 1991). Despite presumably favourable foraging conditions, body condition of few-days-old chicks hatched during rainy periods may thus be poor leading consecutively to retarded growth. In parallel with increasing ability of independent thermoregulation and increasing food and energy requirements, demands on rearing parents should increasingly shift from brooding to food provisioning (Hartwig & Hüppop 1982, Brandl & Nelsen 1988). At the same time, the negative effects of rain should become less significant during chick development but masked and ultimately combined by positive effects as suggested by the present results.

In contrast to precipitation, the effects of wind thought to impair food availability and time budgets of breeding birds during early stages of breeding performance was not confirmed for the pre-fledging period. Resulting from lower predation, survival of nestlings was positively rather than negatively affected by wind during the phase of asymptotic growth. Nevertheless, these effects being apparently contradictory to those mentioned above may also be explained by foraging and provisioning ecology of the gulls studied. Black-headed Gulls are well known as effective kleptoparasites on, for example, tern species. Gorke (1990) as well as Stienen *et al.* (2001) found Black-headed Gulls increasingly kleptoparasitising on Sandwich Terns *Sterna sandvicensis* with progressing chick development and increasing wind speed. A similar effect may be true for the colony studied being associated with Common Terns *Sterna hirundo* which were possibly parasitised by the gulls: Kleptoparasitism increasing with wind speed could have led to positive effects of wind during the phase of asymptotic growth on chick survival.

Thus, important life-history traits such as clutch size and growth rate of chicks as well as breeding output of Black-headed Gulls are related to weather in various different ways. Most of these relationships are most likely ultimately based on variability of foraging conditions dependent on weather. The retarded chick growth in 1996 resulting in a slightly lower breeding success can largely be explained by a relatively dry breeding season (see Fig. 2.2). Nevertheless, there may be some evidence on negative effects even of the preceding ice-winter owing to reduced intertidal prey stocks (Armonies *et al*. 2001). The gulls in this study may use inland grassland habitats as supplemental feeding sites besides tidal flats. Availability of terrestrial prey may depend to a larger extent on temperature, rain and wind than intertidal prey as suggested by Gorke (1990). Presuming these conditions, the relatively poor breeding performance in the 1996 breeding season could have taken place due to a reduced intertidal food supply caused mainly by the ice-winter and a reduced food supply in the supplemental grassland habitat caused by dryness.

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3. Habitatwahl und Schlupferfolg des Rotschenkels (*Tringa totanus*) in landwirtschaftlich genutzten Salzrasen der niedersächsischen Küste

Stefan Thyen

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Abstract

In 1994, habitat selection, habitat use and hatching success of Redshanks breeding in an agricultural salt marsh used at low intensity were studied. The study area consisted of three agricultural plots: an annually mowed meadow, a cattle-grazed pasture and a piece of uncultivated land. 34 breeding-territories were mapped on a vegetation map. Referred to the plant communities an inhomogeneous distribution of the breeding-pairs was found. Abundance of Redshank was higher in an association dominated by orthotropic herbs (*Atriplicetum littoralis*) than in plant communities dominated by grass (*Puccinellietum maritimae, Agropyretum repentis*). A homogeneous distribution on the agricultural plots was found. Measurements of 'vegetation cover', 'vegetation height' and 'heterogeneity of vegetation' at the nest vicinity and 'altitude above sea level', 'distance from ditches' and 'distance from level of mean high tide' of the nests were taken. The birds used particular characteristics of vegetation and topography which varied between habitats. Differences of daily clutch survival probabilities with respect to predation between the pairs breeding in the *Atriplicetum* and the grass communities of the meadow were found. Possible causes of habitat selection and habitat use in Redshank and their significance for meadow bird management in salt marshes are discussed. Furthermore, the significance of habitat use for hatching success and possible influences of agriculture are discussed.

Zusammenfassung

1994 wurden in einem Salzrasen der niedersächsischen Küste Untersuchungen zum Habitatwahl-Verhalten, zur Habitatnutzung und zum Schlupferfolg des Rotschenkels auf landwirtschaftlich extensiv bewirtschafteten Flächen angestellt. Auf drei unterschiedlich bewirtschafteten Parzellen (Brache, Wiese, Weide) wurden die Reviere von 34 Brutpaaren auf Basis pflanzensoziologischer Karten kartiert. Weiterhin wurden an 25 bzw. 27 Brutplätzen und Gelegen Messungen verschiedener Parameter der Vegetationsstruktur und verschiedener topographischer Variablen vorgenommen. Die Vögel brüteten mit signifikant höherer Abundanz in einem von Schaftpflanzen dominierten Vegetationstyp (*Atriplicetum littoralis*), während durch Rasen charakterisierte Habitate weniger dicht besiedelt wurden (Queckenrasen, Andelrasen). Eine durch die extensive Bewirtschaftung zu begründende Habitatwahl wurde nicht gefunden. Hinsichtlich der Nutzung der Habitatstruktur-Parameter traten Unterschiede zwischen den einzelnen Habitaten auf. Die Ursache dieses Phänomens sowie dessen Bedeutung für die Reproduktion der Rotschenkel wird diskutiert. Die tägliche Überlebenswahrscheinlichkeit der Gelege in den einzelnen pflanzensoziologisch abgegrenzten Habitaten und den unterschiedlichen Parzellen landwirtschaftlicher Nutzung war im *Atriplicetum* der Brache höher als in den Rasengesellschaften der Wiese. Die Schlüpfraten unterschieden sich nicht. Die möglichen Einflüsse der Landwirtschaft auf die Brutbiologie der Rotschenkel sowie mögliche Konsequenzen für ein „Wiesenbrüter-Management“ in Salzrasen werden diskutiert.

3.1. Einleitung

Beziehungen zwischen Vegetation und Avifauna wurden bereits vielfach untersucht (z.B. Cyr & Cyr 1979, Erdelen 1984, Becker & Erdelen 1986, Stauss & Glück 1995, Stelte & Sossinka 1996). Viele Arbeiten zur Habitatwahl und -nutzung gehen dabei von einem pflanzensoziologischen Ansatz aus, da die differenzierenden Standortfaktoren und spezifischen Charakteristika der Pflanzengesellschaften oftmals mit den „ultimate factors" der Habitatwahl von Vögeln identisch sind bzw. zumindest mit ihnen als „proximate factors" koinzidieren (s. z.B. Ernsting 1965, Hildén 1965, Rotenberry 1985, Seitz 1989). Auch die Untersuchungen zur vorliegenden Arbeit wurden unter Berücksichtigung pflanzensoziologischer Aspekte durchgeführt, und zwar vor dem Hintergrund der Diskussion darüber, welche Formen von Grünland sog. „Wiesenvögel" als Bruthabitat beanspruchen und ob bzw. wie dieses Grünland zu bewirtschaften ist (Beintema 1975 u. 1986a, Witt 1986, 1991).

Die vorliegende Arbeit thematisiert Einflüsse der extensiven Bewirtschaftung auf die Brutbiologie salzrasenbrütender Rotschenkel. Sie knüpft damit an andere Arbeiten an, die sich mit den Einflüssen intensiver landwirtschaftlicher Nutzung auf Verteilung und Bruterfolg der Vögel des Kulturgrünlandes beschäftigen und meist die Extensivierung, nicht aber die völlige Aufgabe der Bewirtschaftung fordern (vgl. u.a. Matter 1982, Zuppke 1984, Oelke 1985, Ziesemer 1986, Bölscher 1992, Busche 1994, Bairlein & Bergner 1995, Struwe-Juhl 1995a, Schoppenhorst 1996). Mit Blick auf die angestrebte völlige Unterschutzstellung der Deichvorländer des Niedersächsischen Wattenmeeres (Helbing 1992, 1993) wurden in der Vegetationsperiode und der Brutsaison des Jahres 1994 vegetationskundliche und ornithologische Untersuchungen im Nordender Groden (Jadebusen) angestellt. Ziel der Arbeit war es, Qualität und Art einer eventuellen Beeinflussung der Brutbiologie des Rotschenkels durch extensive landwirtschaftliche Nutzung zu ermitteln und Erkenntnisse zu gewinnen, die Prognosen über das Vorkommen der Brutvögel bei Einsetzen von Sukzessionsprozessen nach Aufgabe der Nutzung zulassen.

3.2. Untersuchungsgebiet

3.2.1. Lage und landwirtschaftliche Nutzung

Die Untersuchungen wurden 1994 in einem Grodenabschnitt der Ruhezone des Nationalparks „Niedersächsisches Wattenmeer" durchgeführt, in dem alle drei zulässigen Formen landwirtschaftlicher Nutzung vertreten sind. Im Nordender Groden (südwestlicher Jadebusen; 53°26´ N, 8°10´ E; Abb. 3.1) wurde ein 22 ha großes Gebiet bearbeitet. 32 % dieser Fläche werden nach dem 1. Juli eines Jahres einschürig gemäht (Parzelle „Wiese"), 18 % unterliegen dem Einfluss der Beweidung mit 0,6 Jungrindern/ha (Parzelle „Weide"), 50 % liegen seit spätestens 1986 brach (Parzelle „Brache"). Die bewirtschafteten Flächen erstrecken sich auf einer Breite von 160-320 m in Deichnähe, die Brache schließt in Richtung der Linie des Mittleren Tidehochwassers (MThw) an. Die Beobachtungen beschränkten sich auf das durch MThw-Linie und Deichfuß begrenzte, 400 bis 580 m breite Vorland.

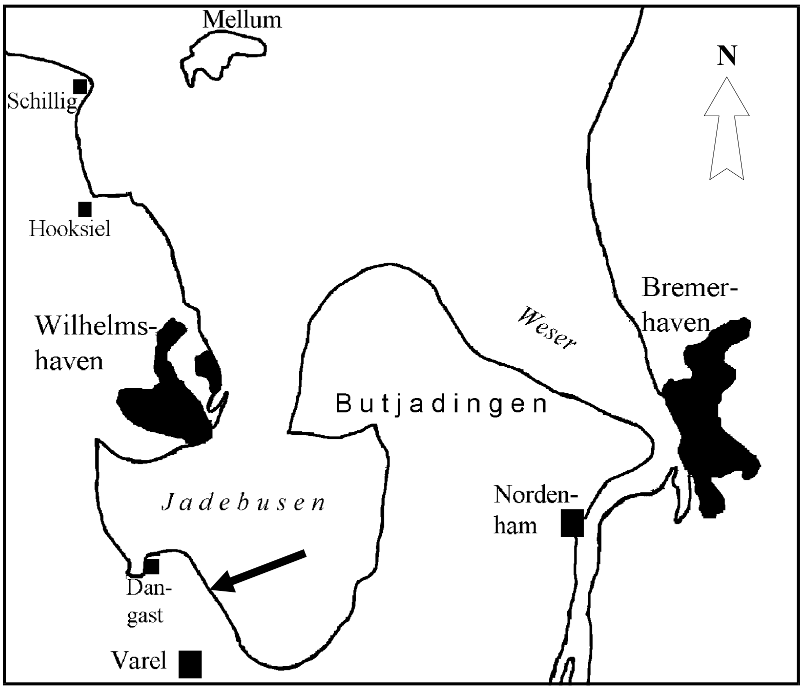

Abb. 3.1: Geographische Lage des Nordender Grodens.
Fig. 3.1: *Geographical location of Nordender Groden.*

3.2.2. Vegetation

Ausgenommen der für Obere Salzrasen typischen Boddenbinsenwiese (*Juncetum gerardii* Nordhagen 1923) sind im Untersuchungsgebiet alle pflanzensoziologischen Komponenten der salzbeeinflussten Pioniergesellschaften und der Salzrasen der Festlandsküste vertreten. Die flächenmäßig wichtigsten Assoziationen sind die folgenden (Nomenklatur nach v. Glahn *et al.* 1989, Beschreibung der Erscheinungsbilder nach Preising *et al.* 1990 bzw. Thyen 1996a):

1. *Salicornietum strictae* Christiansen 55 ex. Tx. 74 – Schlickwatt-Quellerflur

Lockere bis dichte, artenarme Bestände, vornehmlich des Charaktertaxons *Salicornia stricta* (Langähren-Queller). Im Gebiet vertreten in einer bis weit in die Vegetationsperiode hinein überfluteten Senke.

2. *Atriplicetum littoralis* (Warming 06) Feekes 36 em. Westh. & Beeft. 50 – Strandmelden-Spülsaum

Knie- bis hüfthoher, relativ artenreicher, von Strand- und Spießmelde (*Atriplex littoralis, A. prostrata*) dominierter Vegetationstyp. Die Gesellschaft ist einjährig und hat, abhängig vom Auftreten mehr oder weniger ausgeprägter Spülsäume aperiodischer Fluten, temporären Charakter. 1994 war diese Gesellschaft im Untersuchungsgebiet relativ ausgedehnt vertreten.

3. *Puccinellietum maritimae* Christiansen 27 – Andel-Rasen

Relativ niedrig- und dichtwüchsiger, stark von Andel (*Puccinellia maritima*) dominierter und deshalb artenarmer Rasen. Der Aspekt dieser Gesellschaft kann physiognomisch jedoch je nach syntaxonomischer Ausprägung variieren (z.B. *Aster*-Ausbildung des *P. m. typicum* mit ähnlich hohen Beständen wie ein *Atriplicetum*, vgl. Thyen 1996b). Andel-Rasen charakterisieren die im wörtlichen Sinne „Unteren Salzrasen“.

4. *Astero-Agropyretum repentis* von Glahn 86 – Strandastern-Kriechquecken-Rasen
Sehr artenarme, hüfthohe (bis brusthohe), dichtwachsende Vegetationstypen der Kriechquecke. Das *Agropyretum* ist dem „Oberen Salzrasen" zuzuordnen und gedeiht gewöhnlich an sandigen, gut durchlüfteten Standorten der Grabenränder (v. Glahn 1986).

3.3. Methoden

3.3.1. Vegetation, Brutpaar-Verteilung, Schlupferfolge

Die Rotschenkel-Habitate im Brutbiotop Salzrasen wurden über dessen Pflanzengesellschaften definiert. Deshalb wurden zunächst die Vegetationstypen des Untersuchungsgebietes gemäß der Methode nach Braun-Blanquet 1964) bis zur Ebene der Subassoziation differenziert (z.B. *Puccinellietum maritimae typicum; Astero-Agropyretum repentis puccinellietosum*) und in weiteren Schritten auf Biotoptypenkarten der Nationalparkverwaltung „Niedersächsisches Wattenmeer" kartiert 1:2500).

Die Erfassung des Rotschenkel-Brutbestandes und der Brutpaar-Verteilung wurde nach den von Hälterlein *et al.* (1995) vorgeschlagenen Prinzipien vorgenommen, jedoch wurde mit wesentlich höherer Erfassungsintensität vorgegangen: In der Zeit vom 07.04.94 bis 06.07.94 wurde das Gebiet an 32 Tagen durchschnittlich 7 h beobachtet. Darüber hinaus wurde die Fläche regelmäßig zur Gelegesuche und -markierung sowie zur Schlupferfolgskontrolle begangen (nach Exo *et al.* 1996). Durch diese relativ hohe Beobachtungsintensität und durch die Begehungen wurde die Rotschenkel-Population vermutlich quantitativ erfasst (34 Reviere), von 74 % der Brutpaare wurden Gelege gefunden (n = 25) bzw. 27 Brutplätze (77 %) eingegrenzt.

Durch kartographischen Vergleich wurden alle Brutpaare einem durch einen definierten Vegetationstyp charakterisierten Habitat zugeordnet: Die Gelegestandorte bzw. die kartierten „Aktivitätszentren" der Brutpaare wurden als Revier-Mittelpunkte gewertet und dem entsprechenden Vegetationstyp einer Mindestausdehnung von ca. 1000 m^2 zugewiesen.

3.3.2. Habitatstrukturen

Neben der reinen Erfassung der Rotschenkel-Verteilung wurden Messungen zur Nutzung bestimmter Habitatstrukturen vorgenommen:

Die mittlere Vegetationshöhe am Brutplatz wurde aus drei Messwerten aus der direkten Nestumgebung (5 m^2) ermittelt. Die Messungen erfolgten mittels einer kreisrunden Styroporplatte (Durchmesser 30 cm, m = 20 g), die auf die Vegetation gelegt wurde und deren Höhe an einer Meßlatte abgelesen wurde.

Die mittlere Vegetationsdeckung wurde aus Ergebnissen einer am Brutplatz durchgeführten Vegetationsaufnahme abgeleitet. Dazu wurden die geschätzten „Artmächtigkeitswerte" der einzelnen Pflanzenarten (s. Braun-Blanquet 1964) in Werte der „mittleren Deckung" (s. z.B. Dierßen 1990) transformiert und zur mittleren Vegetationsdeckung summiert.

Vegetationshöhen und -deckungen wurden bei Gelegefund ermittelt, also zum Zeitpunkt der Brutplatzwahl der Vögel.

In Anlehnung an eine Methode nach Rotenberry & Wiens (1980) wurde aus den drei Messwerten der Vegetationshöhe für jeden gefundenen Brutplatz ein Heterogenitätsindex zur Beschreibung der Vertikalstrukturierung errechnet. Dieser Index stellt den Quotienten aus der Differenz des höchsten (x_{max}) und des kleinsten (x_{min}) Messwertes und der Summe aller Messwerte (Σ_x) dar. Hohe Indexwerte symbolisieren eine heterogene Vegetationsstruktur.

Nach Abschluss der Brutsaison wurden die Höhen der Neststände ü. NN und deren Entfernungen zu Gräben (natürlich entstandene Priele, künstlich gezogene Grüppen) ermittelt. Durch Nivellement (Nivelliergerät Zeiss Ni 2) wurden die Höhen der einzelnen Nestböden relativ zur Höhe des Höhenfestpunktes 311 des Landesnivellements bestimmt. Die Nest-Graben-Distanz wurde durch Messung der Länge des direkten Weges zum nächstliegenden Graben untersucht.

Die Entfernung der Neststände von der MThw-Linie wurde anhand der Brutvogelkarten berechnet, indem die maßstabgerechte Distanz der einzelnen Neststandorte senkrecht zur MThw-Linie gemessen wurde.

3.3.3. Statistik, Flächenberechnung

Entsprechend des Skalenniveaus der aufgenommenen Daten wurden ausschließlich nicht parametrische Tests angewandt. Verteilungen von Brutpaaren auf Flächen unterschiedlicher Qualität wurden stets per χ^2-Anpassungstest gegenüber dem prozentualen Flächenangebot geprüft.

Alle Tests unterlagen der zweiseitigen Fragestellung.

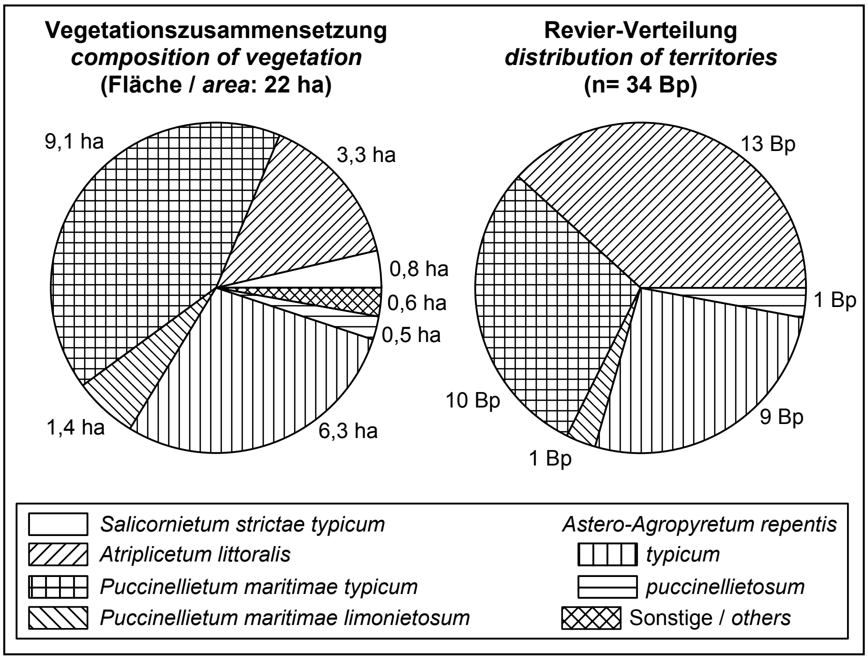

Abb. 3.2: Prozentuales Angebot an Flächen unterschiedlicher Pflanzengesellschaften im Untersuchungsgebiet und Verteilung der Rotschenkel-Brutpaare auf diese Flächen. Bp = Brutpaar(e).
Fig. 3.2: *Supply of various plant communities in the study area and distribution of the Redshank breeding pairs (Bp).*

Die Schlupferfolge wurden nach der Mayfield-Methode (Mayfield 1961, 1975) berechnet und nach Johnson (1979) statistisch bearbeitet. Dabei wurden nur geraubte Gelege als Gelegeverluste gewertet (vgl. Beintema & Müskens 1987). Um ferner auch Verluste durch

Aufgabe von Gelegen oder unbefruchtete Eier zu dokumentieren, wurden die Schlüpfraten als durchschnittliche Anzahl geschlüpfter Küken pro Gelege angegeben.
Die Berechnung der Flächengrößen wurde mit den Programmen des Geographischen Informationssystems der Nationalparkverwaltung „Niedersächsisches Wattenmeer“ bzw. mittels „SigmaScan“ durchgeführt.

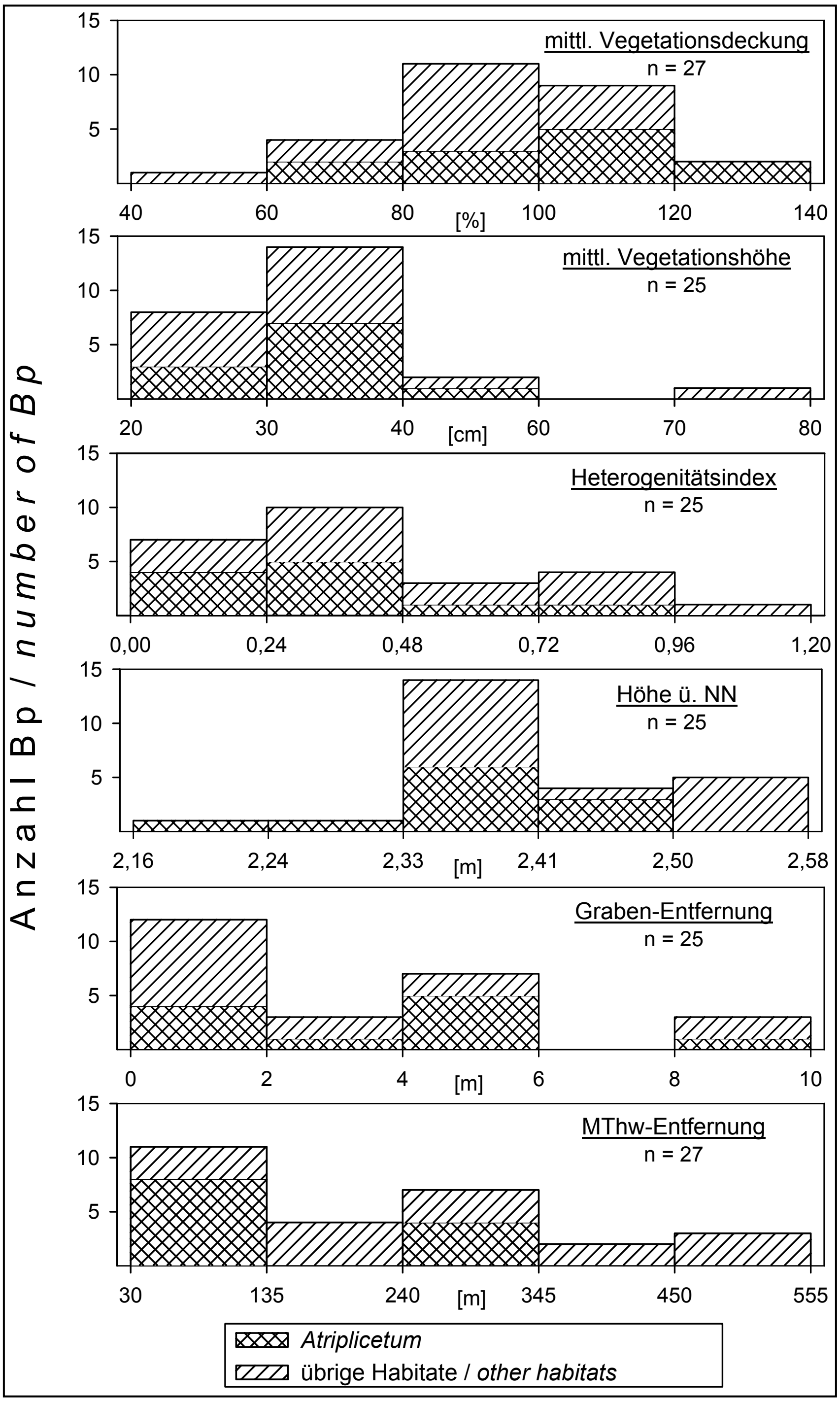

Abb. 3.3: Verteilung der Brutplätze bezüglich verschiedener vegetationsstruktureller Gegebenheiten (drei obere Graphiken) und Verteilung der Neststände in Abhängigkeit von einigen topographischen Parametern (drei untere Graphiken). n = Umfang der Gesamtstichprobe (alle beobachteten Brutpaare), Bp = Brutpaare.

Fig. 3.3: *Distribution of the breeding-sites concerning different characteristics of vegetation structure (three upper graphs) and distribution of the nest-sites regarding several parameters of topography (three lower graphs). n = sample size of whole population, Bp = breeding pairs.*

3.4. Ergebnisse

3.4.1. Habitatwahl der Brutvögel

Die Vögel brüteten im Untersuchungsgebiet mit einer durchschnittlichen Dichte von 1,5 Brutpaaren (Bp)/ha. Die Paare verteilten sich jedoch nicht homogen über die verschiedenen Vegetationstypen des Vorlandes (χ^2-Anpassungstest, $p < 0{,}01$), sondern brüteten relativ häufiger im durch das *Atriplicetum* charakterisierten Bereich (Abb. 3.2). Die Brutdichte betrug hier 3,9 Bp/ha. „Unerwartet selten" brüteten die Vögel dagegen im Andelrasen (*Puccinellietum*; 1 Bp/ha). Gänzlich gemieden wurden die bodenfeuchten Quellerfluren des Gebietes.

3.4.2. Nutzung der Habitatstrukturen

Innerhalb gewisser Spannweiten nutzten die Vögel Brutplätze unterschiedlicher vegetationsstruktureller Ausstattung und Nistplätze unterschiedlicher topographischer Lagen (Abb. 3.3). Vergleichsweise häufig nisteten die Rotschenkel in homogener Vegetation relativ niedriger Höhe und in mittlerer bis hoher Deckung. Die Gelege wurden in erster Linie auf mittleren Höhen ü. NN sowie in der Nähe von Gräben bzw. der MThw-Linie angelegt. Signifikant korrelative Beziehungen zwischen zwei Variablenpaaren wurden nicht gefunden (Spearman-Rangkorrelation).

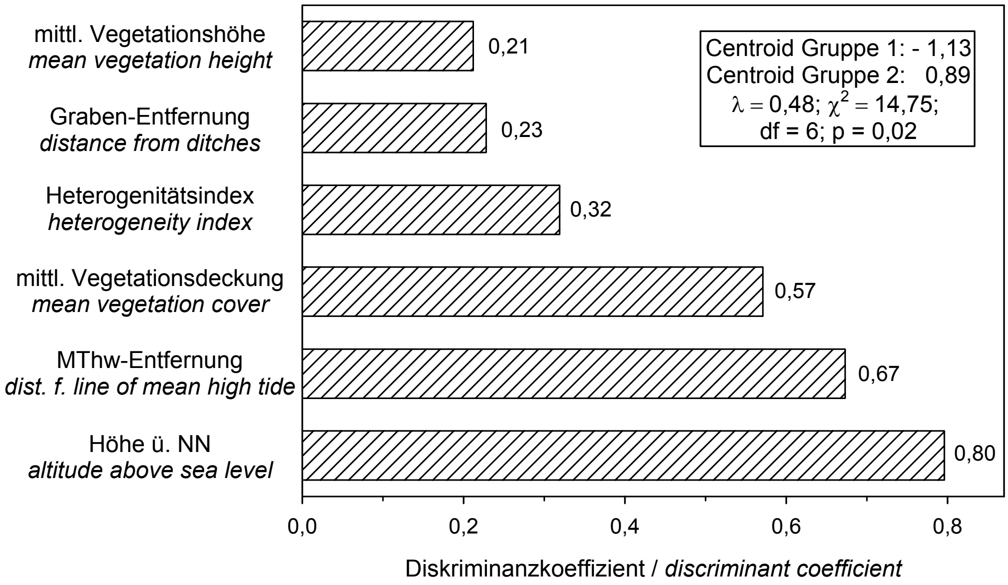

Abb. 3.4: Graphische Darstellung des Ergebnisses einer Diskriminanzanalyse. Analysiert wurden Unterschiede in der Nutzung der untersuchten Habitatstruktur-Parameter durch die Brutpaare des „*Atriplicetum*" (Gruppe 1, n = 11) und der „übrigen Habitate" (Gruppe 2, n = 14). Dargestellt sind die Beträge der errechneten standardisierten Diskriminanzkoeffizienten. λ = Wilk´s Lambda, df = Freiheitsgrade.

Fig. 3.4: *Diagram of the result of a discriminant analysis. The analysis tested whether there are differences in the usage of habitat structures by Redshank breeding in the „Atriplicetum" (group 1, n = 11) and in „other habitats", respectively (group 2, n = 14). λ = Wilk´s Lambda, df = degrees of freedom.*

Nach den Ergebnissen einer Diskriminanzanalyse existieren je nach Habitatzugehörigkeit Unterschiede in der Nutzung der untersuchten Habitatstrukturen (Abb. 3.4). Die Brutplätze und Neststände der Vögel des *Atriplicetum* waren anders strukturiert als die der Paare der übrigen Habitate (p < 0,05). Gemessen an den Diskriminanzkoeffizienten kommt dabei den Variablen „Höhe ü. NN“, „MThw-Entfernung“ und „mittlere Vegetationsdeckung“ die größte diskriminatorische Bedeutung zu (zur Trennung der Gruppen vgl. auch Abb. 3.3). So brüteten die Paare des *Atriplicetum* auf etwas tiefer gelegenen Plätzen, sie zeigten eine gewisse Affinität zur MThw-Linie und ihre Brutplätze waren etwas weniger von Vegetation bedeckt.

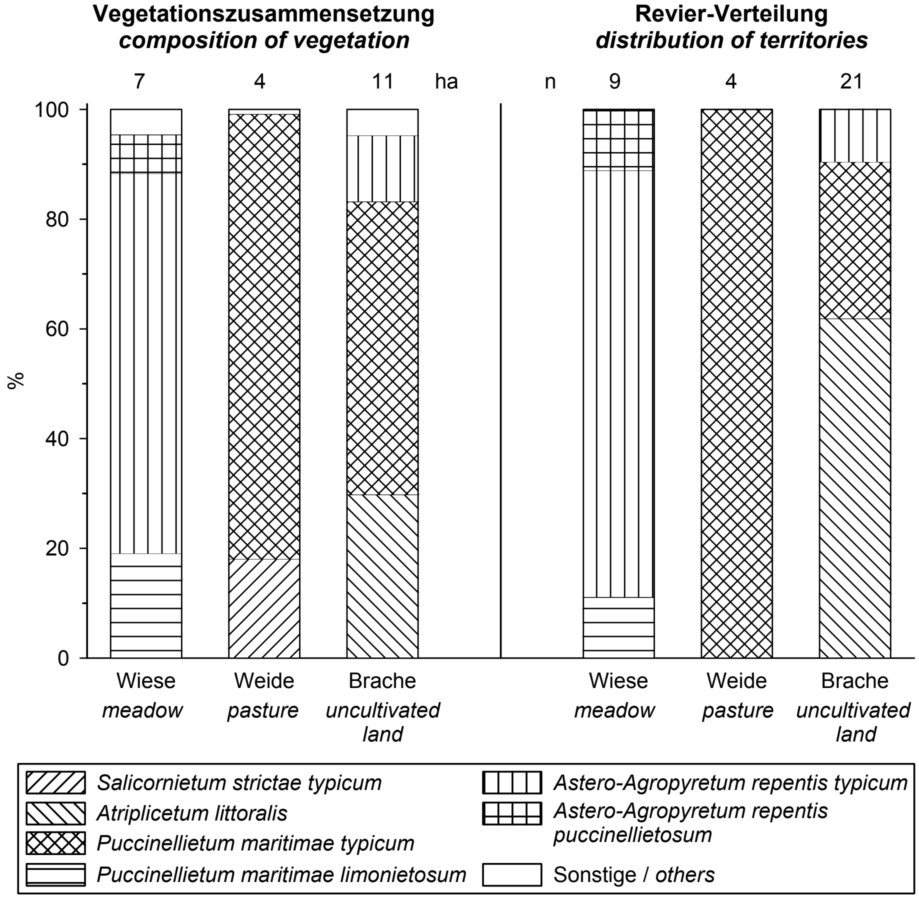

Abb. 3.5: Vorkommen und Verteilung verschiedener Pflanzengesellschaften auf Flächen unterschiedlicher landwirtschaftlicher Nutzung und Verteilung der Brutvögel auf diese Habitate.
Fig. 3.5: *Occurence and distribution of various plant communities on areas of different agricultural usage and distribution of the breeding-pairs.*

3.4.3. Brutpaar-Verteilung auf landwirtschaftlichen Nutzflächen

Mit Ausnahme der Quellerfluren bestand die Vegetation der Wiesen und Weiden nahezu ausschließlich aus Rasengesellschaften. Physiognomisch anders charakterisierte Gesellschaften waren in Form des *Atriplicetum littoralis* nur auf der MThw-nah gelegenen Brache vertreten (Abb. 3.5).

Auf der an unterschiedlichen Vegetationstypen armen Weide brütete der Rotschenkel ausschließlich im Andelrasen, auf der Wiese brüteten die Vögel mit homogener Verteilung in allen Habitaten. Lediglich auf der Brache wurde eine signifikant inhomogene Verteilung gefunden (χ^2-Anpassungstest, p < 0,01): Die Vögel waren hier relativ häufiger im Bereich des *Atriplicetum* zu finden als in anderen Bereichen der Brache und als in allen anderen

Habitaten der übrigen Nutzflächen. Zwischen den einzelnen Parzellen unterschiedlicher Nutzung wurden jedoch keine Abundanz-Unterschiede ermittelt. Die Brutdichten der Wiese (1,3 Bp/ha), der Weide (1 Bp/ha) und der Brache (1,9 Bp/ha) unterschieden sich nicht signifikant (p = 0,36).

Ebenso wenig konnten außerhalb des MThw-nahen Bereichs (135-555 m, vgl. Abb. 3.3) signifikant verschiedene Abundanzen zwischen den einzelnen Habitaten unterschiedlicher Qualität und unterschiedlicher Nutzung nachgewiesen werden: Die Rotschenkel brüteten gleichmäßig über die Untersuchungsfläche verteilt, unabhängig vom Vegetationstyp und unabhängig von der Form der Nutzung.

3.4.4. Schlupferfolge

Signifikante Unterschiede der täglichen Überlebenswahrscheinlichkeiten der Gelege (P) können ermittelt werden, indem geprüft wird, ob der P-Wert einer Stichprobe außerhalb des durch Johnson (1979) als P ± 2 SE definierten 95 %-Konfidenzintervalls einer Vergleichsstichprobe liegt oder nicht. In diesem Sinne unterschieden sich die Gelege-Überlebenswahrscheinlichkeiten der Paare aller Rasengesellschaften nicht voneinander (Tab. 3.1). Im Vergleich mit den Brutvögeln der gemähten Rasengesellschaften wurden aber für die Rotschenkel-Gelege des *Atriplicetum* (Brache) signifikant höhere tägliche Überlebenswahrscheinlichkeiten gefunden (p < 0,05).

Tab. 3.1: Schlupferfolge der Rotschenkel bezogen auf Paare unterschiedlicher Habitate bzw. auf die Gesamtpopulation. P = tägl. Überlebenswahrscheinlichkeit der Gelege nach Mayfield (1961, 1975), SE = Standardfehler nach Johnson (1979), SD = Standardabweichung.

Table 3.1: *Hatching success of Redshank in different habitats. P = daily survival probability according to Mayfield (1961, 1975), SE = standard error according to Johnson (1979), SD = standard deviation.*

Pflanzengesellschaft *plant community*	Nutzung *agricultural use*	n	P ± SE	Küken/Gelege ($\bar{x}$ ± SD) *chicks/clutch*
Rasengesellschaften *grass communities*	Wiese *meadow*	4	0,917 ± 0,056	2,0 ± 2,3
	Weide *pasture*	4	0,958 ± 0,041	2,0 ± 2,3
	Brache *uncultivated land*	4	0,923 ± 0,052	1,5 ± 1,9
Atriplicetum	Brache *uncultivated land*	11	0,957 ± 0,019	1,3 ± 1,7
gesamt / *total*		23	0,948 ± 0,016	1,6 ± 1,8

Signifikant unterschiedliche Schlüpfraten je nach besiedeltem Habitat und je nach dem, auf welcher Parzelle die Vögel brüteten, wurden nicht ermittelt (K-W-Test).

Gelegeverluste durch Viehtritt oder Maschineneinsatz wurden nicht beobachtet. In zwei Fällen wurden Gelege aufgegeben, durch Prädation gingen von 23 untersuchten Gelegen insgesamt zehn verloren.

3.5. Diskussion

3.5.1. Habitatwahl und Habitatnutzung

Nach verschiedenen Modellvorstellungen orientiert sich die Habitatwahl von Vögeln an einem genetisch fixierten und durch Prägung verfeinerten Ökoschema, dessen möglichst genaue Realisierung im Zuge der Habitatwahl angestrebt wird (Hildén 1965, Berndt & Winkel 1974, Cody 1985, Grünberger & Leisler 1993, Glück & Leisler 1993). Ausgehend von dieser Theorie und in der Annahme, dass die Vögel in denjenigen Habitaten mit höchsten Abundanzen vorkommen, in denen sie die subjektiv besten Gegebenheiten vorfinden, kann die im Nordender Groden gefundene Brutpaar-Verteilung des Rotschenkels als Abbild der Attraktivität der verschiedenen pflanzensoziologisch abgegrenzten Habitate gewertet werden.

Wie bei allen anderen Arten ist auch bei Rotschenkeln die Verfügbarkeit der Nahrung der wichtigste „ultimate factor“ der Habitatwahl. Die im Nordender Groden ermittelte hohe Affinität der Brutpaare zur MThw-Linie und die damit offensichtlich angestrebte direkte Nachbarschaft zu den als Nahrungs- und Aufzuchtrevier genutzten Wattflächen dürfte Ausdruck der Ernährungsökologie der Rotschenkel und ihrer Küken sein. Die damit für die Gelege verbundene Überflutungsgefahr wird durch Besiedlung relativ hochgelegener Plätze (z.B. Strandwall) gemieden (vgl. 3.4.2.). Eben diese Räume nimmt auch die Spülsaumgesellschaft *Atriplicetum littoralis* ein. Die Bevorzugung dieser Gesellschaft durch die Brutpaare könnte also auf einer zufälligen Koinzidenz beruhen. Dafür spricht auch die Tatsache, dass die MThw-ferner brütenden Rotschenkel eine von Vegetationstypen unabhängige, homogene Verteilung zeigten (s. 3.4.3.), wobei allerdings das fehlende Angebot an dem *Atriplicetum* ähnlichen Vegetationstypen in diesem Teil des Untersuchungsgebietes zu berücksichtigen ist. Oben beschriebene „Abundanz-Gefälle“ sind auch von anderen Küstenvögeln, z.B. Austernfischer und Seeschwalben, bekannt (Heinze *et al.* 1986, Stock *et al.* 1987, Becker & Anlauf 1988b, Ens *et al.* 1992) und lassen sich sogar auf größere Dimensionen übertragen: In Richtung Binnenland nehmen die Brutdichten der typischen Küstenvögel drastisch ab (Busche 1995, Zang *et al.* 1995).

Auch die mit geringerer Abundanz in größerer MThw-Entfernung brütenden Paare des Untersuchungsgebietes waren offensichtlich bestrebt, zumindest indirekten Zugang zu den Aufzuchtrevieren zu gewährleisten. Die Paare brüteten in der Nähe von Gräben, die mit den Wattflächen in Verbindung stehen und bei Niedrigwasser auch selbst zur Nahrungssuche genutzt werden (vgl. Großkopf 1959, Stock *et al.* 1992).

Für die räumliche Verteilung brütender Rotschenkel im Salzrasen scheint also primär deren Bestreben nach Optimierung der Ernährungs- und Aufzuchtbedingungen verantwortlich zu sein. Für die Optimierung des Bruterfolgs spielt aber auch die Vegetation am Brutplatz eine mehr oder weniger große Rolle (s. auch 3.5.3.). Die im Nordender Groden bezüglich der Nutzung bestimmter Vegetationsstrukturen gefundenen Ergebnisse sind weniger wegen der gemessenen absoluten Höhen und Deckungen der Vegetation am Brutplatz von Interesse. Diese stimmen mit den von anderen Autoren gefundenen weitgehend überein (Glutz von Blotzheim *et al.* 1986, Stiefel & Scheufler 1984, Müller 1994). Bedeutsamer ist der Befund, dass die Vögel verschiedenartige Habitate gewählt und dabei von Habitat zu Habitat variierende Strukturen genutzt haben. Im Hinblick auf die eingangs gestellte Frage nach der

Notwendigkeit von Management-Maßnahmen (extensive landwirtschaftliche Nutzung) dürfte zunächst die Beobachtung, dass die Vögel überhaupt bevorzugt in einer „Nicht-Rasengesellschaft“ gebrütet haben, von großer Wichtigkeit sein (vgl. 3.5.2.).

Nahezu alle MThw-fern siedelnden Brutpaare brüteten in fast ausschließlich aus Gräsern bestehenden Rasen (Andelrasen, Queckenrasen), während die Paare des offensichtlich bevorzugten Habitats in MThw-Nähe hinsichtlich Wuchsform (mehr oder weniger hochwüchsige Schaftpflanzen) und Deckungsgrad anders geartete Pflanzenbestände aufsuchten (vgl. auch Thyen 1996b). Diese Tatsache wirft die Frage auf, ob die Präferenz für den durch das *Atriplicetum* charakterisierten Bereich des Salzrasens auch mit gewissen Strukturpräferenzen übereinstimmt, oder ob in diesem Habitat zugunsten der Nachbarschaft zum Nahrungsrevier suboptimal strukturierte Brutplätze quasi toleriert wurden. Träfe erstgenannte Alternative zu, so wären die Brutplätze der „übrigen Habitate“ hinsichtlich ihrer Vegetationsstruktur suboptimal ausgestattet. Wirkte sich diese suboptimale Ausstattung auf die Schlupf- und damit die Bruterfolge der Rotschenkel aus, wovon nach verschiedenen Autoren auszugehen ist (s. u.), so wären damit Einflüsse der Landwirtschaft neuer Qualität aufgedeckt (s. 3.5.3.). Träfe dagegen letztgenannte Alternative zu, so könnte sich dieses Verhalten ebenfalls negativ auf die Schlupferfolge auswirken. Diese negativen Auswirkungen könnten möglicherweise aber durch einen relativ höheren „Aufzuchterfolg“ ausgeglichen werden.

3.5.2. Einflüsse der Landwirtschaft auf die Habitatwahl

Von der extensiven Nutzung des Außengrodens scheinen keine positiven Effekte auf Verteilung und Vorkommen der Rotschenkel auszugehen. Abgesehen von den wattnahen Bereichen verteilten sich die Paare des Nordender Grodens homogen über den Salzrasen, ohne genutzte oder brachliegende Flächen zu bevorzugen (3.4.3.). Diese Beobachtung steht zunächst zu den Annahmen verschiedener Autoren im Widerspruch, dass Grünland durch extensive Nutzung als Wiesenbrüter-Biotop zu erhalten und zu pflegen sei. Zweck eines solchen Managements soll die Hemmung von Sukzessionsprozessen sein (Verstaudung, Verbuschung, Bewaldung), mit denen eine zunehmende „Wiesenbrüterfeindlichkeit“ einhergeht (Beintema 1975, 1982, 1986a, 1986b, Gerdes 1988, 1990, Bölscher 1992, Eikhorst & Mauruschat 1996).

Derartige Maßnahmen sind im Hinblick auf die Besiedlungsfähigkeit von Salzrasen-Biotopen offenbar nicht notwendig, was insofern nicht überrascht, als Salzrasen zu den ursprünglichen Brutbiotopen des Rotschenkels und anderer Wiesenbrüter zählen. Im übrigen sind „Wiesenbrüter“ vor diesem Hintergrund objektiver als „Brutvögel des Grünlandes“ zu bezeichnen (Glutz von Blotzheim *et al.* 1986, Witt 1986). Der Grund für dieses Ergebnis dürfte mit dem Kompromiss zusammenhängen, den Rotschenkel und vergleichbare Arten in binnenländischem Grünland eingehen müssen: Aus Gründen des Sichtschutzes muss die Vegetation bis zu einem gewissen Grad entwickelt sein, darf aber nicht zu hoch und nicht zu dicht sein, soll die edaphische, epigäische oder epiphytobiotische Nahrung für Adulte und Jungvögel erreichbar sein (Beintema *et al.* 1991, Struwe-Juhl 1995b, Rottenborn 1996). Die Rotschenkel des Salzrasens dagegen nutzen externe Nahrungs- und Aufzuchtreviere und können deshalb durchaus auch höhere und dichtere Vegetationstypen nutzen. Im

Untersuchungsgebiet wurden niedrige Andelrasen ebenso besiedelt wie hohe Queckenrasen und relativ hochwachsende Strandmelden-Spülsäume. Daraus dürfte folgen, dass auch Gesellschaften fortgeschrittener Sukzessionsstadien (z.B. *Artemisietum,* Strandbeifuß-Gesellschaft) mit anderer als der im Binnenland durch Pflege angestrebten rasenartigen Physiognomie von Rotschenkel-Brutpaaren genutzt werden, zumal gerade diese Vegetationstypen bevorzugt an Grabenrändern wachsen (vgl. Stock *et al.* 1992, v. Glahn *et al.* 1989). Aus den Ergebnissen folgt weiterhin, dass offensichtlich keine der gräserdominierten Gesellschaften durch die Bewirtschaftung in irgendeiner Form eine Veränderung erfährt, die die Attraktivität dieser Gesellschaft für die Rotschenkel steigern würde (s. 3.4.3.).

Die Salzrasen-Nutzung mit dem Ziel eines Wiesenbrüter-Managements erübrigt sich nach diesen Ergebnissen, da zu vermuten ist bzw. im Falle der vieldiskutierten Queckenrasen (z.B. Bakker & Ruyter 1981, Gerdes 1990, Bakker 1993a, b) hiermit auch nachgewiesen ist, dass alle vorkommenden Sukzessionsstufen (zu denen im übrigen keine Gehölzformationen zählen; Briemle *et al.* 1991, Ellenberg 1996) vom Rotschenkel genutzt werden können. Da Salzrasen mehr oder weniger zoniert sind, qualitativ und physiognomisch verschiedenartige Vegetationstypen also nebeneinander existieren und nicht flächendeckend einander ersetzen, dürfte ein solches Management ebenso wenig für die anatomisch und ethologisch anders ausgestatteten Offenbrüter, wie Austernfischer und Kiebitz, notwendig sein (Thyen 1996b).

3.5.3. Schlupferfolge des Rotschenkels

Verschiedene Autoren haben auf die Bedeutung bestimmter vegetationsstruktureller Eigenschaften der Bruthabitate für die Schlupferfolge der Vögel hingewiesen. Schlupferfolge können je nach Nistverhalten ebenso inter- wie intraspezifisch variieren, und zwar auf Grundlage verschiedener Mechanismen (z.B. Prädationsschutz, mikroklimatische Bedingungen am Gelege; Beintema & Müskens 1987, Picman 1988, Berg *et al.* 1992, Martin 1994, Mitchell *et al.* 1996).

Rotschenkel benötigen zur Anlage eines adäquaten Nestbaus Vegetation, die eine versteckte Brut ermöglicht, zugleich aber freie Rundumsicht gestattet (Stiefel & Scheufler 1984). Im Nordender Groden brüteten die Vögel in unterschiedlich strukturierter Vegetation. In Extremfällen wurden Gelege sowohl in homogen hoher Vegetation ohne die Möglichkeit der freien Sicht angelegt, wie auch in sehr niedrigen Beständen, wobei die Vögel mit abnehmender Vegetationshöhe offenbar zunehmend auf Kleinstrukturen angewiesen waren, etwa in Form vereinzelter Rotschwingelhorste (*Festuca rubra litoralis*) in ansonsten monotonem Andelrasen. Auch wenn die Schlupferfolg-Ergebnisse der vorliegenden Arbeit eher Anlass zu weiteren Untersuchungen sein sollten als dafür, definitive Schlüsse zu ziehen, so lassen diese Ergebnisse doch vermuten, dass die Nutzung verschiedenartiger Vegetation durchaus den Schlupferfolg beeinflussen kann (3.4.4.). Deshalb scheint auch ein indirekter Einfluss der Landwirtschaft auf die Reproduktionserfolge der Vögel wahrscheinlich. Grundsätzlich beeinflusst intensive wie extensive Landwirtschaft nämlich die vegetationsstrukturelle Ausstattung des Grünlandes: Die Nutzung be- oder verhindert die herdenartige Ausbreitung höherwüchsiger Schaftpflanzen, vielmehr werden phänologisch und morphologisch an die Nutzungsperiodik angepasste Pflanzen gefördert. Beweidung wie Mahd verhindern damit die Ausbildung von „Mikrogrenzen“, also mehr oder weniger reich vertikalstrukturierter Vegetation (Irmler & Heydemann 1986, Dierßen *et al.* 1991, Briemle & Schreiber 1994, Ellenberg 1996).

Die Besiedlung der Queckenrasen der Wiesen wie der „golfrasenähnlichen“ Weiden (v. Glahn *et al.* 1989) des Nordender Grodens könnte somit auf Kosten der Möglichkeit rechtzeitigen Feindverhaltens bzw. auf Kosten einer ausreichenden Tarnung erfolgt sein. Zumindest tendenziell spiegelt sich diese Theorie in den Überlebenswahrscheinlichkeiten der Gelege wider, die für die in den Rasengesellschaften der Wiese gezeitigten Gelege kleiner war als für das *Atriplicetum*, das ausschließlich auf der Brache vertreten war.

Der Zusammenhang zwischen „landwirtschaftliche Nutzung“ des Salzrasens, „Veränderung der Vegetation durch die Bewirtschaftung“ und „Vorkommen und Reproduktionserfolg der Rotschenkel“ im Salzrasen ist demnach also ein anderer als das entsprechende Gefüge auf Kulturgrünland des Binnenlandes. Der Salzrasen ist in ernährungsökologischer Hinsicht hochattraktiv, weswegen Einflüsse der extensiven Bewirtschaftung auf das Habitatwahl-Verhalten der Rotschenkel nicht existieren (s. auch Schultz 1987). Die Vögel brüten auch in monotonen Rasengesellschaften (die zwar auch Teil des unkultivierten zonierten Salzrasens sind, aber unter dem Einfluss der Landwirtschaft eine starke Ausdehnung erfahren), obwohl in Vegetationstypen mit höherwüchsigen Therophyten und Stauden mit einiger Wahrscheinlichkeit höhere Schlupferfolge erzielt werden. Anders als für Grünland-Biotope des Binnenlandes muss im Falle des Salzrasens also davon ausgegangen werden, dass extensive Nutzung nicht nur „keine positiven Effekte auf das Vorkommen der Vögel“ hat (s. 3.5.2.), sondern dass darüber hinaus negative Effekte auf den Bruterfolg dieser Vögel existieren.

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4. Interactive Effects of Time and Vegetation on Reproduction of Redshanks *Tringa totanus* Breeding in Wadden Sea Saltmarshes

Stefan Thyen and Klaus-Michael Exo

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Abstract

As proved in various species, nesting waders are non-randomly distributed on wetlands and preferably select riparian nest-sites adjacent to limnic or marine waterbodies. We tested the hypotheses that in a coastal wader species, which conceals the clutch in vegetation, predation and hatching success are affected by vegetation zonation and that breeding in lower salt marsh areas has negative consequences for reproduction. We furthermore predicted effects of timing of breeding and breeding experience/age of adults potentially reflected by egg biometrics both on nest-site selection and reproduction. Effects of vegetation, space, time and individual quality on hatching success of redshanks *Tringa totanus* were studied in the German part of the Wadden Sea. Dominant plant species, vertical vegetation structure and nest concealment varied significantly between nests. Variation in nest concealment was relatively low: about 90 % of clutches were classified as being well concealed. This variation was explainable only by vegetation structure but not by vegetation composition at nest-site, distance to shoreline, and time of clutch initiation. Vertical vegetation structure varied by dominant plant species but not by distance to shoreline and time of clutch initiation. Hatching success of clutches was low (10.6 %) due to high predation (daily predation rate: 7.4 %). Hatching success and duration of clutch survival were negatively and predation positively related to date of clutch initiation. Furthermore, negative relationships were found between eggs size and predation and duration of survival, respectively. We assume that concealed, early breeding and breeding experience diminish predation in salt marsh breeding redshank. Thus, redshank reproduction appears to be affected by interactive effects of timing of breeding and vegetation facilitating early breeding. In contrast to open-nesting species, breeding in riparian habitats next to waterbodies may be disadvantageous for species breeding concealed in vegetation if these are covered by less structured vegetation.

4.1. Introduction

The choice of an appropriate nesting habitat including a well suited nest-site is one of the most important life-history decisions of birds. Habitat and, as a subset of that, nest-site selection is a behavioural response to various proximate cues aimed to meet the life-history needs of individuals (ultimate factors of habitat selection), e.g. to maximise reproductive success. In general, nesting-habitat and nest-site selection are characterised by several trade-offs to guarantee a habitat with sufficient food supply and a nest-site safe against predation and adverse weather. Different habitats are sequentially filled, with high quality habitats (i.e. those which guarantee highest reproduction) occupied first and with higher densities than poorer ones (Hildén 1965; Cody 1985; Bernstein *et al.* 1991; Newton 1998). Besides intraspecific competition, selection of nesting-habitats can be frequently explained by further inter- and intraspecific interactions within a community such as associative breeding, and temporal and spatial predator avoidance (Lack 1968; Newton 1998).

Nesting-habitat selection of many wader species may also be characterised by another trade-off between selecting a habitat near supra- or eulittoral foraging territories and selecting a nest-site which is safe against flooding. Many wader species display a heterogeneous distribution on breeding habitats caused by competition for preferred nesting sites adjacent to limnic or marine waterbodies (e.g. Grover and Knopf 1982; Ens *et al.* 1992; Thyen 1997; Milsom *et al.* 2000). Access to feeding sites and inaccessibility of nest-sites for ground predators are assumed to be important proximate cues promoting this distribution. For example, in Eurasian oystercatchers *Haematopus ostralegus*, nesting next to tidal flats can have positive consequences for reproduction due to improved access to foraging territories for chicks as well as brooding adults (Ens *et al.* 1992). Nevertheless, it is questionable if breeding next to waterbodies in limnic and marine habitats is generally advantageous for breeding success of waders. At least at relatively undisturbed sites, nesting habitat is characterised by zonated or patchy vegetation of different composition and structure according to elevation and succession (Ellenberg 1996). Since predation is a main factor restricting breeding success of birds and since many bird species have to rely on concealing their clutch in vegetation to protect it passively from predation (Ricklefs 1969; Nilsson 1984; Bennett & Owens 2002), hatching and breeding success of less aggressive species susceptible to predation should vary with succession. In the case of zonated European salt marshes, potentially less productive and less structured early succession stages of lower salt marshes (e.g. *Puccinellia*-communities) are located nearer to tidal flats than those of upper salt marshes (e.g. *Festuca*-, *Elymus*-communities) (Ellenberg 1996). Thus, hatching success of species dependent on concealing their clutch in vegetation should increase temporarily with succession and spatially with zonation and distance to shoreline.

Derived from these considerations, the hypothesis was tested that salt marsh succession affects nest predation and hatching success of species concealing their nest in vegetation. The study was conducted on redshanks *Tringa totanus* breeding in the Wadden Sea. Similar to oystercatchers, salt marsh breeding birds of this species feed mainly on tidal flats. In contrast, chicks appear to remain within salt marsh foraging territories until fledging (Großkopf 1959; Glutz von Blotzheim *et al.* 1986; Thompson *et al.* 1990). Compared to that of many other coastal birds, redshank anti-predator response is relatively ineffective, resulting in a higher dependence on cover and camouflage of clutches in appropriate vegetation (Glutz von Blotzheim *et al.* 1986). Therefore, during nest-site selection in salt marshes, redshanks are possibly forced to trade-off between selecting less concealed nest-sites near potential foraging territories and selecting well concealed sites relatively far from these territories (see above). Habitat selection of redshank is relatively well known, whereas reproductive consequences of this selection are poorly studied. Several studies have shown higher abundance of pairs in *Elymus*- and other upper salt marsh plant communities compared to those of lower salt marshes (Norris *et al.* 1997; Thyen 2000; Esselink 2000). Thyen (1997, 2000) found that redshank hatching success varied among salt marsh habitats according to vegetational, physiognomic and topographic parameters. However, the means by which these habitat parameters affected hatching success could not exactly be defined. Hence, in the present more detailed study, effects of nest-site characteristics on redshank reproduction were examined by testing the following assumptions: We assumed that hatching success was higher in relatively well structured vegetation of advanced succession stages compared to vegetation of early succession. It consequently was predicted that hatching success increases spatially by distance of nests to shoreline in accordance with the chronosequence of vegetation reflecting succession. To discriminate between effects of vegetation and spatial habitat parameters and those originating from individual quality, effects of timing of nest initiation and of egg biometrics potentially reflecting body mass and/or age of adults (Großkopf 1958; Thompson and Hale 1991) were studied additionally. We predicted that high quality nest-sites (i.e., potentially those of advanced succession stages, see above) not only provide higher hatching success but were occupied earlier and by potentially more experienced birds (as indicated by egg biometrics) than low quality sites.

4.2. Methods

4.2.1. Study area

The studies were conducted on the salt marshes of the Southern Jadebusen (53°26´ N, 8°05´ E), Wadden Sea National Park of Lower Saxony, Germany, in 2000 and 2001. With approx. 2 pairs*ha^{-1}, the study site has one of the highest redshank breeding abundance in Central Europe (Rasmussen *et al.* 2000; Thyen and Exo 2003). Mustelids, rodents and carrion crows (*Corvus corone corone*) occurred as potential egg predators, herring gulls (*Larus argentatus*) and red foxes (*Vulpes vulpes*) were less abundant (Thyen and Exo 2004). 15 % of the area was covered by a pit from which clay was removed for dike-building. This pit was characterised by muddy sediments. According to biotope maps from 1997, 60 % of the study area (60 ha) were characterised by *Puccinellion maritimae* plant communities ("lower salt marsh") and 25 % by *Armerion maritimae* communities ("upper salt marsh") (classification according to Pott 1992). However, this proportion changed towards a considerably higher share of *Armerion* communities dominated by, for example, *Elymus repens, Festuca rubra* ssp. *litoralis*, and *Elymus athericus* vs. *Puccinellion* communities characterised by species such as *Puccinellia maritima, Triglochin maritimum* and *Plantago maritima* in 2000/2001 (nomenclature according to Wisskirchen & Haeupler 1998). Owing to the lack of updated vegetation maps, current areas of plant communities are not known.

About 30 % of the area described above was agriculturally used at a relatively low intensity (cattle grazing and mowing by 50 % each). Grazing intensity was 1 cattle/ha as from May, mowing was conducted once a year in July.

4.2.2. Recording of nest-site characteristics and hatching success

Searching, marking and inspection of nests were performed according to Exo *et al.* (1996) and Thyen *et al.* (1998) during mid-April to the end of June. Inspection intervals were 6 (2000) and 7 (2001) days as a rule but varied between 4 to 7 days mainly due to weather conditions. 90 nests were recorded altogether. However, in several cases nests could not be visited regularly due to adverse weather or high tides. Identical samples could therefore not always be taken for all parameter measurements leading to slightly different sample sizes between parameters.

On finding a nest, nest-sites were mapped using a GPS receiver (Garmin GPS 12). Sites were characterised by composition and vertical structure of vegetation and concealment of nests. Vegetation composition was recorded on about 4 m^2 around the centrally lying clutch applying the Braun-Blanquet (1964) approach (Thyen 1997). Vegetation structure was recorded during the visit following clutch finding. A vegetation stratimeter (Oppermann 1989) was used consisting of an infrared light transmitter panel and a receiver panel arranged in parallel. The stratimeter measured relative transmission of pulsating infrared light through a defined volume of vegetation, i.e. 24 cm (gap between transmitter and receiver panel) * 43 cm * 10 cm (surface of panels). At each nest, 10 measurements of 10 cm layers from ground to 100 cm above the nest were performed. Vegetation coverage in different layers above the nest can be derived directly from these measurements. Concealment was determined by measuring light intensity within the nest cup directly above the eggs during early morning hours (6:00 – 9:00). Measurements were conducted on intact, concealed nests using a luxmeter whose probe was shaded during each measurement. To get a reference value, comparative measurements 1 m above the nests were taken (see below).

Since redshanks are nidifugous birds, only hatching but not breeding success could be determined by regular nest inspections (Exo *et al.* 1996; Thyen *et al.* 1998). During each inspection, the status of clutches was recorded. To determine fates of clutches as accurately as possible, estimates of hatching date were calculated from egg biometrics (see below). Egg length, breadth and mass were measured using a calliper (precision ± 1 mm) and an electronic balance (precision ± 0.1 g). Clutches were classified as being lost or hatched if nests were found empty before or after the estimated hatching date, respectively. In addition, nests of hatched clutches often were still well concealed and small egg shell fragments could be found inside the nest. In a few cases, hatching success could be directly determined by holes and cracks in egg shells indicating imminent hatching or by nestlings found in the nest. In case of clutch predation, nests often were opened and relatively big egg remains with rests of yolk could be found in the nest vicinity. We did not determine predator species on the appearance of egg remains due to unreliability of results (Larivière 1999). Clutches were classified as being deserted if eggs were found cold and damp at two successive inspections. Causes of desertion could not be determined. Losses due to flooding and cattle trampling could easily be recognised by definite traces such as mud, hoof tracks and crushed eggs in the nest.

4.2.3. Data analysis and statistics

Three variables characterising nest-sites were derived from the measurements described above. “Dominant plant species” is defined as the species with highest “cover-abundance index” (Braun-Blanquet 1964) in the vegetation record of a nest-site. In 93 % of records, cover-abundance index of dominant species indicated a horizontal coverage between 25 % and 100 % (Mühlenberg 1989). To reduce the number of variables describing vertical coverage of nest-site vegetation and, thus, to simplify analyses, a “vertical coverage index” was derived from the vegetation stratimeter measurements. Vertical coverage index is defined as the mean coverage of the three variables revealed as contributing significantly to the discrimination of nest-sites, i.e. coverage of the layers 20-30 cm, 30-40 cm and 40-50 cm above the nest (see Results). Furthermore, a “nest concealment index” was calculated from luxmeter measurements. It is defined as light intensity within nest in % of surrounding daylight measured 1 m above the nest.

To study spatial aspects of nest-site selection, effects of distance to shoreline on hatching success were examined. Distance to shoreline was determined by calculating the nearest distance of the nest to the shoreline using a geographical information system (ArcView 3.2a).

Besides vegetation and spatial parameters of nest-sites, some supplementary parameters on timing of breeding and egg biometrics were analysed. Since clutches were mostly found after completion, hatching dates were estimated by egg biometrics according to the method given by Green (1984) (446508 * mass (g) * length^{-1} (mm) * breadth^{-2} (mm) – 197). From observed clutches surviving the incubation period, precision of this method was about ± 2 days. Date of clutch initiation was calculated by the minimum estimated hatching date of eggs * clutch^{-1} – 24 d (which is the average duration of incubation according to Glutz von Blotzheim *et al.* 1986). To guarantee comparability between the two study years, "relative date of clutch initiation" was calculated by relating dates of clutch initiation to the first laid clutch of a season whose date of initiation was set to 0. "Duration of clutch survival" was calculated by subtracting the date of clutch initiation from the date of clutch loss or hatching. As far as the date of clutch loss or hatching was not definitely known, the date was determined by the method given by Mayfield (1961). Duration of clutch survival is defined as % of the total incubation time of 24 d.

Besides the parameters directly measured (see above), egg volume was calculated by 0.51 * length * breadth^2 (Hoyt 1979). All analyses including egg biometrics are based on means per clutch.

Daily survival probability (DSP), daily predation rate (DPR) and hatching success were calculated according to Mayfield (1961). Standard error of DSP was calculated according to Johnson (1979). Pairwise comparisons of DSP were made using the method given by Hensler and Nichols (1981). It was assumed that the incubation period of redshanks lasts 24 d and that all eggs of a clutch experienced the same fate. Except for a very few cases, the latter assumption was verified during fieldwork. No reliable discrimination between first and replacement clutches could be made. Thus, hatching success is related to clutches rather than to breeding pairs.

Statistics were performed according to Jongmann *et al.* (1995), Backhaus *et al.* (1996) and Sachs (1997) applying SPSS for Windows 10.0 statistical package. In some analyses, metrically scaled variables needed to be grouped. Vertical coverage index and nest concealment index were classified by cluster analyses (Ward method, squared Euclidean distance) and subsequently tested by discriminant analyses. Distance of nest to shoreline, date of clutch initiation, and egg biometrics were classified in three groups which were distinguished by 33 % and 67 % percentiles. To analyse effects of vegetational and spatial nest-site characteristics on hatching and predation of clutches, multiple logistic regression models were applied. All multivariate analyses were applied by entering predictor variables simultaneously. In case of parametric tests, nest concealment index and duration of clutch survival were arcsine square root transformed and log-transformed, respectively, to generate homogeneity of variances and normal distribution. All other variables included in parametric tests met the test assumptions without transformation. All tests were two-tailed.

4.3. Results

4.3.1. Vegetational nest-site characteristics

46 % of all 90 redshank nest-sites studied were dominated by *Elymus repens*, 31 % by *Festuca rubra* and 14 % by *Puccinellia maritima*. The vegetation of the remaining nest-sites (9 %) was dominated by *Plantago maritima*, *Triglochin maritimum*, *Aster tripolium* or *Elymus athericus*.

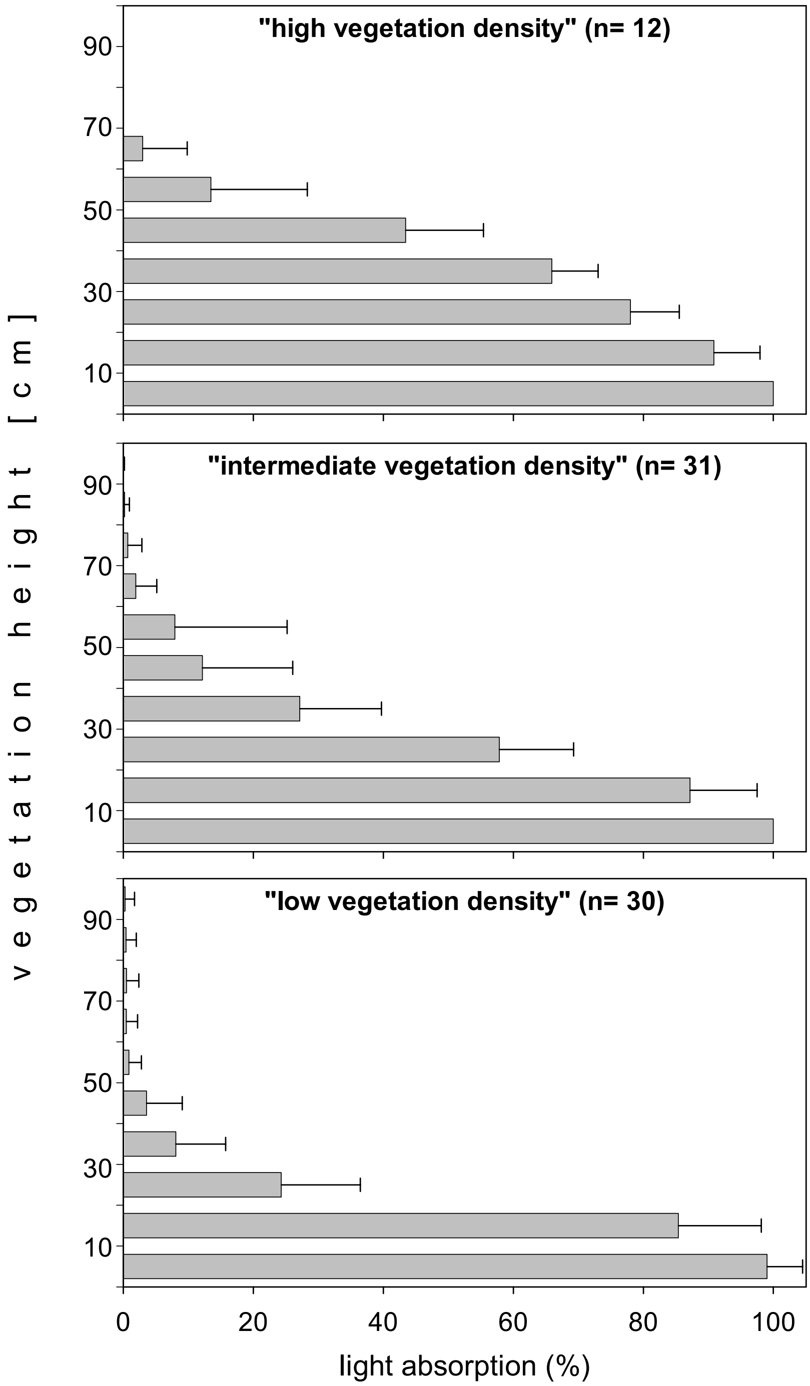

Fig. 4.1: Vertical vegetation structure at three groups of Redshank nest-sites differentiated by a cluster analysis. For each vegetation layer above the nest, mean relative light absorption ± SD is presented indicating the vegetation coverage of the respective layer. n = number of nests.

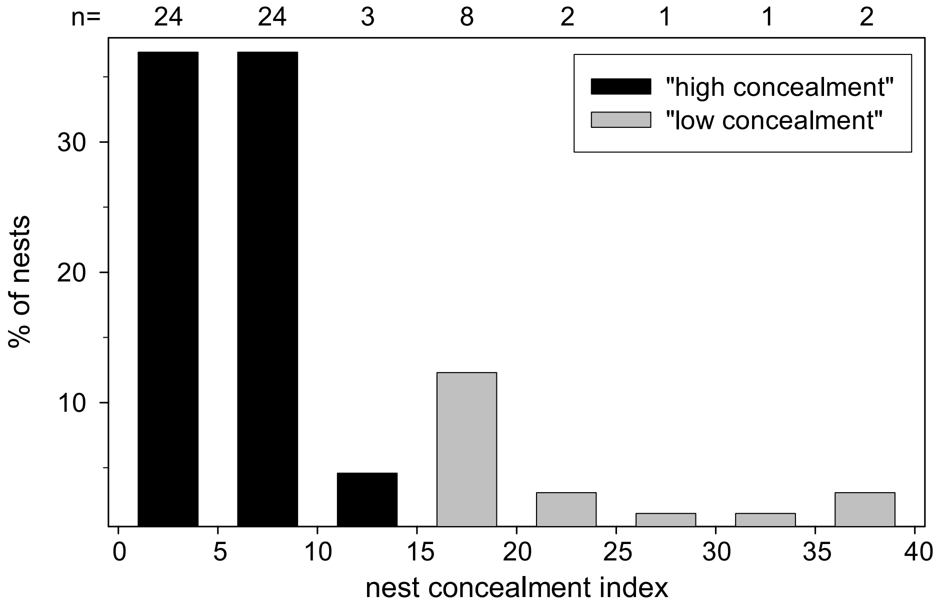

Fig. 4.2: Frequencies of Redshank nests of different concealment and discrimination of the nests as revealed by a cluster analysis. Nests not classified (5 of 69) by the analysis are not considered.

All measured nest-sites (n = 73) could be classified by a cluster analysis in three groups of significantly different vertical vegetation structure (discriminant analysis: function 1: χ^2 = 176.67, df = 20, p < 0.001; function 2: χ^2 = 37.34, df = 9, p < 0.001) (Fig. 4.1). Similarly, 95 % of 69 measured nests could be grouped in well and less concealed ones (discriminant function: χ^2 = 76.37, df = 1, p < 0.001) (Fig. 4.2).

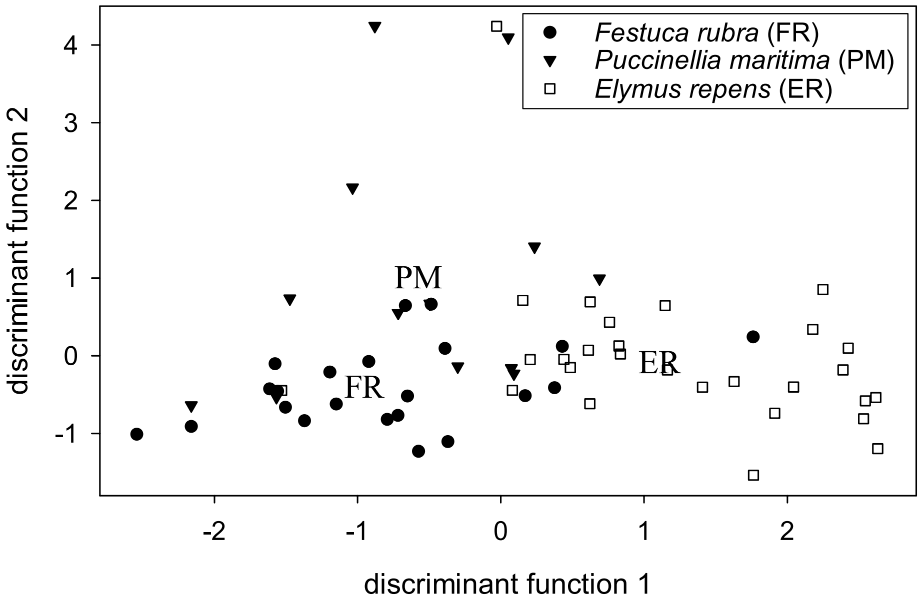

Fig. 4.3: Results of a discriminant analysis separating Redshank nest-sites dominated by different salt marsh grasses by variables of vertical vegetation structure (nine variables of vertical vegetation coverage of 10-cm-layers between 10 and 100 cm vegetation height, cf. Fig. 4.1) and nest concealment. Abbreviations indicate group centroids.

Nest-sites dominated by different grass species could be separated by physical parameters (Fig. 4.3). As revealed by a discriminant analysis (function 1: χ^2 = 57.45, df = 20, p < 0.001;

function 2: $\chi^2 = 14.73$, df = 9, p = 0.099), vegetation coverage of the three layers between 20 and 50 cm height above the nest contribute significantly ($p < 0.001$ each) to discrimination of nest-sites characterised by different grass species. In the respective layers, vegetation coverage was denser at *E. repens*-sites (60.2 ± 15.7 % to 22.4 ± 20.0 %) than at sites dominated by *F. rubra* (29.4 ± 21.1 % to 4.6 ± 10.0 %) or *P. maritima* (37.9 ± 19.3 % to 6.2 ± 7.1 %). In contrast, nest concealment index made no significant contribution to discrimination of nest-site groups defined by dominant plant species (F = 0.22, df1 = 2, df2= 67, p = 0.802). However, there was a significant positive relationship between vertical coverage indices of nest-sites and nest concealment (linear regression: $y = 6.13 + 0.10x$, $R^2 = 0.07$, p = 0.032, n = 69).

Table 4.1: Survival and hatching success of redshank clutches in 2000 and 2001 discriminated by different variables. Data from both breeding seasons were pooled for analyses. N = number of nests, ED = exposure days, DSP = daily survival probability of nests, DPR = daily predation rate of nests, HS = hatching success (each according to Mayfield 1961), SE = standard error (according to Johnson 1979). See text for classification of grouping variables (cf. Figs. 4.1 and 4.2). Superscript characters indicate significant differences ($p \leq 0.05$) in DSP among groups as calculated according to Hensler and Nichols (1981).

Group	N_{total}	N_{failed}	$N_{predated}$	ED	DSP ± SE	DPR	HS (%)
total	83	71	59	796	0.911 ± 0.010	0.074	10.6
dominant plant species at nest-site							
A *P. maritima*	13	12	10	93	0.871 ± 0.035	0.108	3.6
B *F. rubra*	25	22	17	258	0.915 ± 0.017 ^{d}	0.066	11.8
C *E. repens*	37	29	25	413	0.930 ± 0.013 ^{d}	0.061	17.4
D other species	8	8	7	32	0.750 ± 0.077 ^{b,c}	0.219	0.1
vertical coverage index							
A high	10	8	7	116	0.931 ± 0.024	0.060	18.0
B intermediate	29	25	20	258	0.903 ± 0.018	0.078	8.7
C low	29	26	22	253	0.900 ± 0.019	0.087	7.4
nest concealment index							
A high	49	41	34	445	0.908 ± 0.014	0.076	9.8
B low	12	12	11	83	0.855 ± 0.039	0.133	2.4
distance to shoreline							
A near	24	24	21	169	0.858 ± 0.027 ^{b,c}	0.124	2.5
B intermediate	34	27	22	376	0.928 ± 0.013 ^{a}	0.059	16.7
C far	25	20	16	251	0.920 ± 0.017 ^{a}	0.064	13.6

4.3.2. Spatial variability of nest-site characteristics

Distance of nests to shoreline did not vary between nest-sites characterised by different dominant plant species (Kruskal-Wallis-test: $\chi^2 = 4.87$, df = 2, p = 0.088, n = 77). Distance to shoreline was not correlated with either nest concealment index (rank correlation analysis: $r_S = 0.09$, p = 0.458, n = 69), vertical coverage index ($r_S = 0.22$, p = 0.071, n = 73) or relative date of clutch initiation ($r_S = 0.08$, p = 0.516, n = 85).

4.3.3. Effects on hatching success and duration of clutch survival

In 2000 and 2001, hatching success of redshank was low due to high clutch predation. No interannual difference in DSP was found (Table 4.1; Hensler and Nichols test: Z = 0.12, p = 0,904). Besides predation, desertion of clutches (5.5 % of all clutches found), trampling by cattle (3.3 %) and flooding (2.2 %) were further causes of clutch losses. DSP and hatching success was relatively high at nest-sites dominated by *Festuca* and *Elymus* and at sites relatively far from the shoreline. Variations in daily predation rate were reverse. No variations in DSP by vertical coverage index and nest concealment index were found.

A multiple logit regression analysis revealed no effect of “dominant plant species at nest site”, “vertical coverage index”, “nest concealment index” and “distance to shoreline” on survival or predation of clutches ($p > 0.150$ each). Similarly, neither duration of survival of all clutches nor that of depredated clutches was affected by vegetation and spatial variables according to an ANCOVA ($p > 0.150$ each).

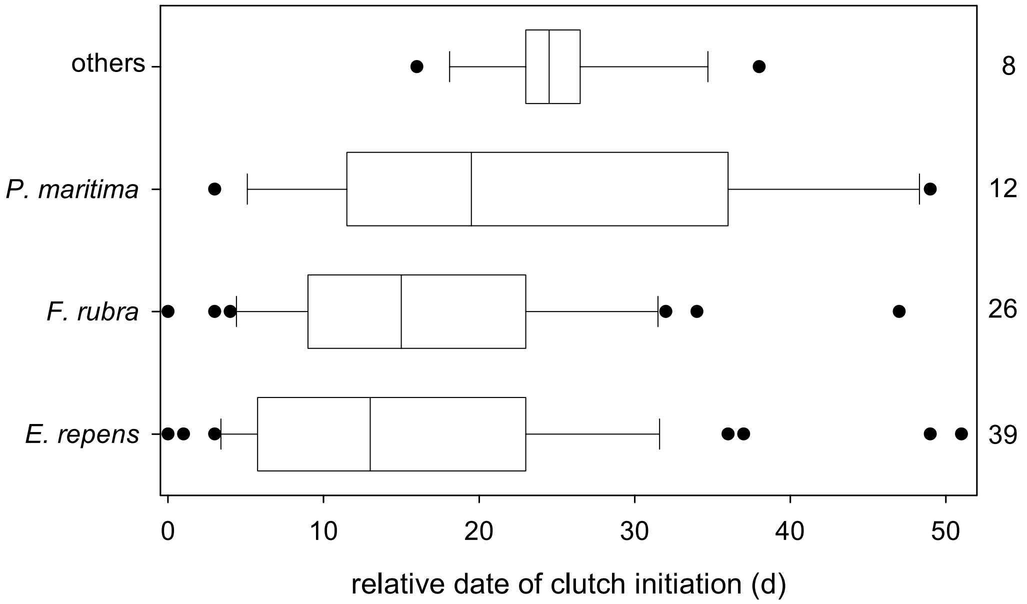

Fig. 4.4: Relative dates of clutch initiation at nest-sites characterised by different dominant plant species. See text for species comprised by “others”. Whiskers indicate 10 and 90% percentiles, left and right boundaries of boxes mark 25 and 75% percentiles, lines within boxes represent medians, numbers right from the graph: n per group.

4.3.4. Variability and effects of timing of breeding

Relative date of clutch initiation did not vary significantly by dominant plant species at nest-sites (Kruskal-Wallis-test: $\chi^2 = 2.34$, df = 2, p = 0.310, n = 77). However, clutches found at *Elymus*- and *Festuca*-sites tended to be produced earlier than those at *Puccinellia*-sites (Fig. 4.4). In addition, no relationships between relative date of clutch initiation and vertical coverage index (linear regression: p = 0.693, n = 73) and nest concealment index (p = 0.224, n = 69) respectively were found.

DSP of clutches laid early in the breeding season was considerably higher than that of those laid later whereas DPR varied oppositely (Fig. 4.5). As revealed by logit regression analyses, hatching of clutches (n = 69) was negatively (B ± SE = -0.13 ± 0.05, $R^2 = 0.23$, p = 0.008) and clutch predation positively (B ± SE = 0.65 ± 0.03, R^2 = 0.13, p = 0.012) affected by date of clutch initiation (Fig. 4.6). Additionally, clutches laid relatively early within the season survived for a longer period than those laid relatively late even if they were depredated later in the season (linear regression: all clutches: y = 70.02 – 1.02x, R^2 = 0.18, p < 0.001, n = 80; depredated clutches: y = 53.8 – 0.64x, R^2 = 0.12, p = 0.008, n = 59).

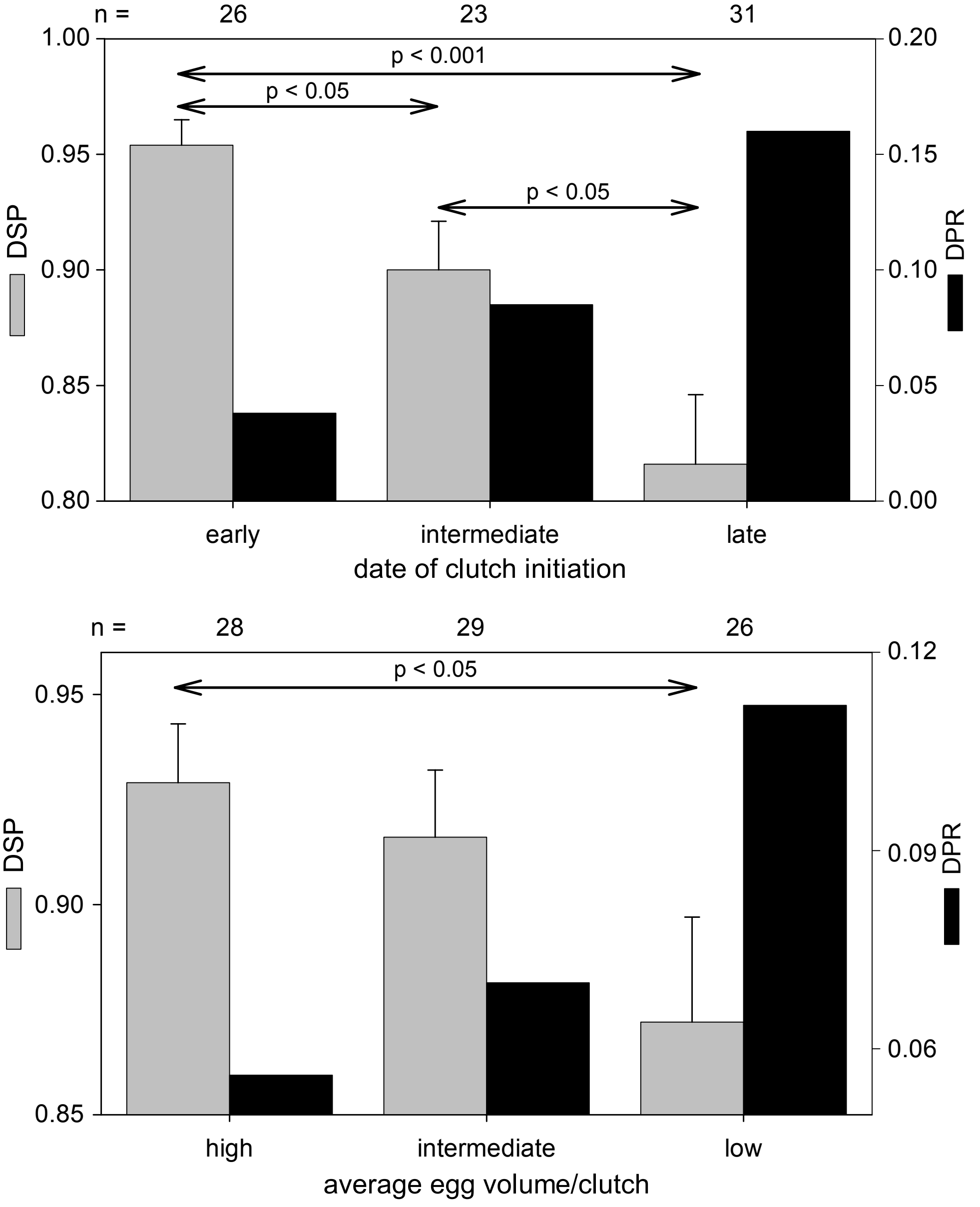

Fig. 4.5: Daily survival probability (DSP) ± SE and daily predation rate (DPR) of groups of Redshank nests distinguished by date of clutch initiation (upper graph) and average egg volume * clutch $^{-1}$. n = number of observed clutches per group. Arrows indicate significant differences among groups as calculated according to Hensler and Nichols (1981).

4.3.5. Variability and effects of egg biometrics

Egg biometrics varied between nest-sites characterised by different dominant plant species and with initiation date but not with distance to shoreline, vertical coverage index and nest concealment index (Table 4.2). Eggs found at *F. rubra*-sites were heavier than those at *P. maritima*-sites (21.6 ± 1.3 g vs. 20.5 ± 1.5 g; Scheffé test: p = 0.048; *E. repens*: 21.0 ± 1.5 g).

Average egg volume * clutch^{-1} was negatively related to date of clutch initiation (linear regression: y = 22.5 – 0.03x, R^2 = 0,06, p = 0.029, n = 85).

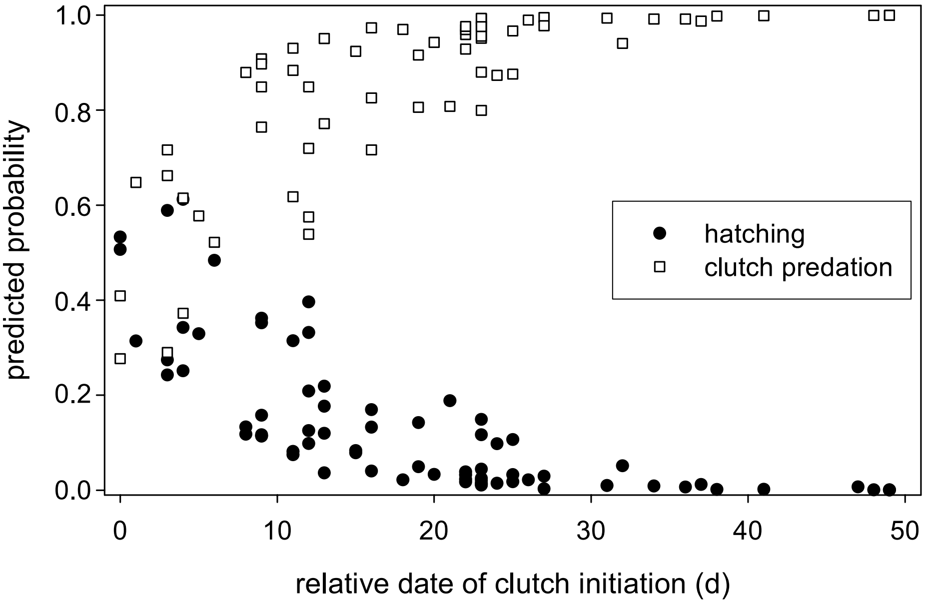

Fig. 4.6: Relationships between date of clutch initiation and hatching probability and nest predation probability, respectively, as predicted by logit regression analyses. Clutch losses different from predation were excluded from the analysis examining predation.

Clutches with relatively high average egg volumes had a higher DSP and a lower DPR than those with relatively light eggs (Fig. 4.5). Significant positive relationships between egg biometrics and duration of survival of depredated clutches were found (linear regression: average egg mass * clutch^{-1}: y = -53.1 + 4.45x, R^2 = 0.07, p = 0.05, n = 59; average egg volume * clutch^{-1}: y = -91.8 + 6.03x, R^2 = 0.13, p = 0.005, n = 59). Depredated clutches with relatively heavy and big eggs survived for a longer period than those with smaller eggs. No comparable results were found for duration of survival of all clutches.

Table 4.2: Results of two ANCOVAs examining variations in egg biometrics by vegetational, spatial and temporal nest-site characteristics. N = 69 nests found in 2000 and 2001. Variables on vertical coverage, nest concealment, distance to shoreline and date of clutch initiation were included in analyses as covariates. Effects of interactions among independent variables were not considered.

	df	Average egg mass per clutch		Average egg volume per clutch	
		F	p	F	p
dominant plant species at nest-site	2	3.04	0.035	2.15	0.102
vertical coverage index	1	1.02	0.317	0.56	0.455
nest concealment index	1	1.42	0.237	0.81	0.371
distance to shoreline	1	1.71	0.195	1.77	0.188
relative date of clutch initiation	1	2.65	0.108	4.12	0.046

4.4. Discussion

The results suggest that the consequences of nest-site selection for reproduction of redshank depend slightly on vegetation succession: hatching success appears to increase with chronosequence and distance to shoreline. However, this variation cannot directly be explained by composition and structure of vegetation. The results suggest that hatching success rather depends on timing of breeding and individual quality of breeders. Succession, composition and structure of salt marsh vegetation may nevertheless be of substantial importance for redshank reproduction by providing specific requirements on nest-sites (e.g. structure as proximate cue for concealment) and by interacting with timing of breeding.

4.4.1. Causal and functional aspects of nest-site selection

Although nest-site selection of redshank was not studied but rather consequences of this selection, the present results permit some interesting insights into its causation. One of the most fundamental findings is that nest concealment varied only slightly between nests (approx. 89 % of nests were classified as being “well concealed”) and that variation in concealment was not explicable by distance of nests to shoreline, time of clutch initiation and vegetation composition. Instead, concealment was explainable by vegetation structure which in turn did not depend on distance to shoreline and time within breeding season. These facts suggest firstly not that concealment itself is a proximate cue promoting nest-site selection but more likely vegetation structure of the potential nest-site. Furthermore, neither phenology nor zonation nor space *per se* are obviously responsible for selection of nest-sites in salt marsh-nesting redshank. The factors causing this selection are possibly random, adaptive or “extrinsically induced”. On the one hand, they could be related to a sufficient supply of suitable territories with respective nest-sites and/or a relatively narrow intrinsically fixed requirement of redshank on concealment of potential nest-sites. The high predation pressure found in the study area is on the other hand a third possible explanation for the findings mentioned above. Even if constraints on foraging ecology of incubating and chick rearing adults cannot be excluded, breeding far from the shoreline in well structured vegetation may be a kind of “predator avoidance strategy” forced by high predation pressure. As many other bird species, redshanks can learn from reproductive failure and react by shifting nest-site location in the following season (Thompson and Hale 1989). Furthermore, there are several examples for birds breeding non-randomly distributed (Burger 1985; Tryjanowski *et al.* 2002) or in more concealed locations (Newton 1998) in response to predator occurrence. Though, experience-based learning forced by high predation-pressure in former seasons is hardly a plausible explanation for the nest-site selection found in the study area: egg mass and volume, assumed to reflect age and/or breeding experience of adults (Thompson and Hale 1991), did not vary between sites of different vegetation structure and concealment. Thus, experienced birds probably did not select more concealed nest sites than less experienced ones. Additionally, it may be difficult for birds to perceive and assess predator occurrence prior to nest-site selection and breeding (Sutherland 1996). This should be particularly true if predation pressure is highest later in the breeding season as it appeared to be in the present study (see below). These considerations as well as the relatively high redshank breeding pair abundance found in the study area (Rasmussen *et al.* 2000; Thyen and Exo 2003) are arguments against an effect of predation pressure on nest-site selection and, thus, the nest-site characteristics found.

Salt marsh-nesting Eurasian oystercatchers prefer breeding near tidal flats with positive consequences for breeding success due to optimal access to intertidal foraging territories (Ens *et al.* 1992). In redshank, neither a comparable “spatial affinity” to tidal flats nor positive consequences of breeding next to tidal flats for reproduction could be proved. At least in terms of hatching success, which may not be representative for breeding success, for redshank it appears to be more likely disadvantageous to breed in areas near tidal flats if these are covered by *Puccinellia*-communities (see below). Since there was a strong influence of predators on hatching success, the questions arise if selecting nest-sites in obviously attractive salt marshes under high predation pressure is a kind of “ecological trap” or if there are mechanisms besides nest-site selection guaranteeing sufficient hatching and breeding success.

4.4.2. Effects of nest-site characteristics on predation and hatching success

Since predation is a major cause of breeding failure in birds, many species should camouflage or conceal their nest from predators to increase fitness (Ricklefs 1969; Nilsson 1984; Collias and Collias 1984; Bennett & Owens 2002). However, many studies have failed to prove any effect of nest concealment on predation and offspring survival. Most authors attribute this phenomenon to a negative relationship between intensity and efficiency of anti-predator behaviour of parents and nest concealment (“optimality theory of nest defence”). The real effect of nest concealment may be masked by an adjusted adult behaviour varying inter- as well as intraspecifically (Götmark *et al.* 1995; Cresswell 1997; Weidinger 2002; Burhans *et al.* 2002). In other studies, an absence of an effect of nest concealment on offspring survival was attributed to the occurrence of incidental rather than actively searching predators (Vickery *et al.* 1992; Schmidt *et al.* 2001). Thus, besides habitat and nest-site characteristics, studies on nest predation should ideally include further parameters, e.g., parental behaviour and predator-prey interactions (Schmidt 1999).

For hatching success of salt marsh-breeding redshank, it should be advantageous to breed relatively remote from the shoreline at well structured and well concealed sites in upper (*Elymus, Festuca*), rather than in lower, salt marsh vegetation (*Puccinellia*) to reduce predation. However, similar to the studies cited above, neither a spatial variation in nest concealment nor relationships between hatching success and predation and concealment were found. Rather, hatching success and predation were strongly related to timing of breeding. The absence of significant effects of nest concealment on predation could partly be explicable by the activity of olfactorially searching or incidental species such as mustelids (*Mustela* spp.) and rodents (*Microtus/Apodemus* spp., *Rattus norvegicus*). However, there should be further mechanisms explaining these findings.

Early breeding in birds is commonly assumed to increase post-fledging survival and fitness by increasing experience, social status, body condition, etc. of offspring (Nilsson 1999). Götmark (2002) showed that offspring of great tits (*Parus major*) benefit from early breeding by avoiding an increased food demand of breeding sparrowhawks (*Accipiter nisus*). A similar effect is conceivable in redshank. All species observed as potential egg predators have young at the end of April/beginning of May (Niethammer and Krapp 1978; Glutz von Blotzheim & Bauer 1993; Stubbe & Krapp 1993a; b). Thus, food demand of predators should be high even at the beginning of the redshank breeding season (end of April) but it should increase during development of predator nestlings. Since probability of clutch predation was highest from about 25 days after start of the season (> 0.9, see Fig. 4.6), early breeders should have a relatively good chance to incubate successfully. Thus, early breeding and temporal avoidance of highest predation pressure may be one aspect of successful incubation of redshank breeding in a predator-rich environment. However, there are further possible explanations for temporal variations in predation and hatching success as suggested by the results that early nests are not only more successful but resist predators for a longer period even if they are depredated later in the season. These explanations may include behavioural mechanisms such as active defence, nest guarding and nest attentiveness. The findings of Thyen *et al.* (2002) being comparable to those of Sasvári and Hegyi (2000) may be evidence to such mechanisms. Redshank clutches were unattended for a considerable share of time (about 33 % of a day). Frequency and duration of off-duty periods varied diurnally and during the season. These findings led to the conclusion that this behaviour might have been a strategy of incubation induced by high predation pressure.

Thus, in salt marshes strongly affected by different predator species, incubating successfully could be based on a complex framework of nest-site supply and various behavioural responses of redshank to environmental conditions. Within this framework, temporal and vegetation parameters may interact since early breeding requires appropriate, i.e. well concealed, nest-sites even early in the season which are apparently provided especially by upper salt marsh vegetation (*Elymus, Festuca*) (cf. Esselink 2000). However, it is unclear whether redshank behaviour is indeed a response to the conditions described. Again egg biometrics may give some information about this question. Egg mass did vary between nest-sites of different vegetation composition and egg volume was negatively related to time of clutch initiation, similar to the findings of Summers & Underhill (1991). These results may suggest that especially experienced birds of good body condition start breeding early in the season (cf. Großkopf 1958; Großkopf 1970; Thompson and Hale 1991; Summers & Underhill 1991). This may be a response to former unsuccessful breeding attempts relatively late in the season. In this framework, prospection of one-year old breeders and floating and queuing could play an important role even in redshank reproduction (cf. Großkopf 1970; Thompson and Hale 1989; Kokko and Sutherland 1998).

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5. Monitoring Breeding Success of Coastal Birds

Final Report of the Pilot Study 1996 – 1997

Stefan Thyen, Peter H. Becker, Klaus-Michael Exo, Bernd Hälterlein,
Hermann Hötker and Peter Südbeck

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Abstract

In the framework of the 'Trilateral Monitoring and Assessment Program' (TMAP), pilot studies on monitoring breeding success of coastal birds were carried out in 1996 and 1997. As part of the TMAP, a methodological concept was developed 1992 until 1994. This concept provides to study hatching and breeding success and body mass development of chicks of selected coastal bird species. By means of monitoring breeding success, the state of the marine environment of coastal birds is supposed to be supervised and ecological changes within the ecosystem are supposed to be recognised. In addition, the monitoring program is expected to be used together with "monitoring population size of breeding birds" and "monitoring chemicals in seabirds" as an "early warning system" in coastal bird protection.

The aim of the pilot study was to evaluate the practical applicability of the methodological draft and to assess the value of the recorded data for the Wadden Sea conservation in general and especially for the future integration of the parameters of breeding success into the TMAP.

Studies were carried out on the target species Herring Gull (*Larus argentatus*), Black-headed Gull (*L. ridibundus*), Common Tern (*Sterna hirundo*), Oystercatcher (*Haematopus ostralegus*), and Avocet (*Recurvirostra avosetta*). On the one hand, these species are characteristic birds of the Wadden Sea, on the other hand, they are distinguished by different breeding and feeding strategies. The qualitatively different study areas were located throughout the total area of the German part of the Wadden Sea.

Both, hatching success and breeding success varied in three different ways. Except for a few cases, the colonial species achieved higher hatching success than the territorial Oystercatcher. Higher hatching success was usually found at breeding places located on islands than at those located on the mainland. Except for the Herring Gull colonies at all sites, Black-headed Gulls on Langeoog and Common Terns on Minsener Oog, hatching success always was higher in 1997 than in 1996, mostly caused by a decrease in predation. Breeding success varied similarly but only in Black-headed Gulls and in Avocets, a different breeding success was found between years. Both species bred more successful in 1997 than in 1996.

Due to methodological reasons, the development of chicks was only studied in the three larid species. Especially in the case of Black-headed Gulls, an increased chick mortality was found in 1996 compared to 1997. In nearly all species, study sites, and years, maxima of chick mortality were found in the middle of June and towards the end of June, respectively. Whereas the growth pattern of Herring Gull chicks was similar at all regions and in both years, Black-headed Gull nestlings grew with lower rates and without any regional differences in 1996 than in 1997. More than two-week-old Common Tern chicks at Minsener Oog were lighter in 1996 than in 1997.

Body mass development of the young indicate that there was an annually varying food supply. A reduced benthic food supply in 1996 in comparison to 1997 is discussed which could have caused lower hatching and breeding success of Black-headed Gulls, Avocets, and Oystercatchers. As a possible reason for the assumed shortage of benthic food in 1996, the 'ice-winter' in 1995/1996 is discussed. Furthermore, possible connections between the weather and the mortality of all larid chicks are discussed as well as influences of the availability of young fish in the North Sea on the growth of Common Terns in 1996.

The value of the results for Wadden Sea conservation, for coastal bird conservation, and for the trilateral Wadden Sea monitoring program is discussed. The following items are concluded from the practical experiences and results achieved during the pilot study: 1. The method is well applicable and yields exact results concerning the breeding biology and the annual avian reproductivity. 2. Monitoring breeding success is able to supervise the state of the marine environment of coastal birds and also of the Wadden Sea as a whole. Therefore, monitoring breeding success is to establish as an essential part of the TMAP. 3. Monitoring breeding success can be used as an "early warning system" for negative changes in coastal bird population sizes. An effective conservation of the coastal avifauna only seems to be guaranteed by establishing a long-term project and by conducting the program in connection with monitoring population size and monitoring chemicals in seabirds. 4. The program is suited to determine "natural breeding success" of birds and to measure natural and anthropogenic deviations.

Thus, monitoring breeding success is not only a very useful, but even an essential tool to achieve the trilaterally adopted "Ecological Targets".

5.1. Introduction

The Wadden Sea is one of the last natural and extensively preserved zonal ecosystems of Central Europe (Kaule 1991). From the ecological as well as from the spatial point of view, it has to be regarded as one functional unity. An effective conservation of this ecosystem requires a co-operation of all states bordering on the Wadden Sea, i.e. Denmark, Germany, and the Netherlands. Therefore, regular meetings of the responsible ministers at the 'Trilateral Governmental Wadden Sea Conference' have taken place since 1978 on the political level. On the scientific level, co-operative ecological research is carried out. In 1994, the ministerial conference agreed on common aims ("Ecological Targets", abbreviated to "Ecotargets" in the following report) to achieve the full scale of habitat types which belong to a natural and dynamic Wadden Sea. In case of breeding and migrating birds, favourable conditions like a favourable food availability, a natural breeding success, sufficiently large and undisturbed roosting and moulting areas, and natural flight distances have to be guaranteed (Bakker *et al.* 1997).

Monitoring the state of the environment by observing the features of sensitive life communities is an important tool of diagnostic ecological research, and the use of this tool is essential for the preventive conservation of nature and environment (Baillie 1990, Kaule 1991, Plachter 1991, Bairlein 1995). In face of the demands for effective mechanisms of early recognition of negative changes within the ecosystem (e.g. Kempf *et al.* 1987, Leendertse *et al.* 1992, Stock 1992, Asmus *et al.* 1994, Lozán *et al.* 1994), the trilateral Wadden Sea Conference confirmed the urgency of monitoring the Wadden Sea in 1991. The 'Trilateral Monitoring and Assessment Program' (TMAP) was consequently established in 1994 (CWSS 1995). In the framework of this program, the 'Trilateral Monitoring Expert Group' (TMEG) evaluated several 'Issues of Concern' from a large scale of possible man-made influences on the Wadden Sea ecosystem which should have priority in the monitoring program. It is intended to reveal impacts of climate change, contamination and eutrophication, commercial fisheries, recreation, and agricultural practice on the Wadden Sea ecosystem by examining different parameters (e.g. biological parameters, chemical parameters, etc.). By implementing these projects, the functioning of ecological feed back mechanisms are supposed to be observed and assessed in order to achieve the Ecotargets (CWSS 1995).

Seabirds and coastal birds are organisms of a high trophic level and an extreme mobility which use a large range of the Wadden Sea habitat resources (pelagial, eulittoral, semi-terrestrial and terrestrial habitats). Therefore, these organisms are very sensitive concerning environmental changes caused by different sources. The special qualification of these birds as indicators as well as the particular attention and effort of protection they get is based on this sensibility (Furness 1987, Becker 1991, 1993a, 1993b, Furness & Greenwood 1993). Even before the TMAP was established, the ‘Joint Monitoring Program for Breeding Birds in the Wadden Sea’ started surveying systematically breeding bird population sizes at the North Sea coast (Hälterlein *et al.* 1995, Hälterlein & Südbeck 1996, Melter *et al.* 1997). This project is an important instrument to assess the current state of the avifauna of the Wadden Sea. Environmental changes, however, can be indicated earlier and more effective by declining breeding success of coastal birds being K strategists than by declining population sizes. Thus, monitoring breeding success is a kind of “early warning system”. Its “signals” (e.g. for food shortage, for environmental pollution, etc.) enable specific studies on causal connections as well as the timely performance of suitable countermeasures prior to population declines (Furness & Monaghan 1987, Becker 1992, Becker *et al.* 1997a).

The implementation of monitoring breeding success started with the elaboration of a methodological guideline (Exo *et al.* 1996). This concept prescribes the annual observation of the reproductive success of birds with different breeding habitats and different breeding and feeding strategies by applying defined methods. Adopted on a trilateral level, Herring Gulls (*Larus argentatus*), Black-headed Gulls (*L. ridibundus*), Common Terns (*Sterna hirundo*), Oystercatchers (*Haematopus ostralegus*), and Avocets (*Recurvirostra avosetta*) were selected as indicator species. Furthermore, the observation of Redshanks (*Tringa totanus*) was intended initially. However, this intention was rejected because of the high time expenditure needed to find clutches and the disturbances involved.

In 1996 and 1997, the method was used for the first time synchronously in the framework of a trilaterally adopted pilot project in Lower Saxony and Schleswig-Holstein. The aim was to test the applicability of the methods and to assess the value of the TMAP-parameter “breeding success” as a component of an early warning system (see above). The results of the two-year project are presented and discussed in this report.

5.2. Study areas

As prescribed by the methodological instructions, the monitoring was conducted at representative breeding places and colony sites which are characterised by potentially different ecological qualities (Fig. 5.1, Table 5.1). Breeding places on islands and on the mainland, at exposed sites and in bays, at marine and limnetic influenced regions (Elbe, Beltringharder Koog, Fahretofter Koog) were selected as well as pastures and uncultivated land of the salt marshes on the mainland. The agricultural use of salt marshes in Schleswig-

Holstein is usually limited to intensive sheep-grazing, whereas in Lower-Saxony cattle-grazing and mowing at low intensity (e.g. at Augustgroden) is permitted. Except for the foreland of Neßmersiel in 1996, not the whole study areas, but strips of about a few hundred meters adjacent to the dike were agriculturally used (e.g. Augustgroden: 300 m). Some bird species prefer breeding adjacent to the tidal flats. Thus, birds breeding in used salt marshes are not necessarily under the direct influence of agricultural activities (see Table 5.1).

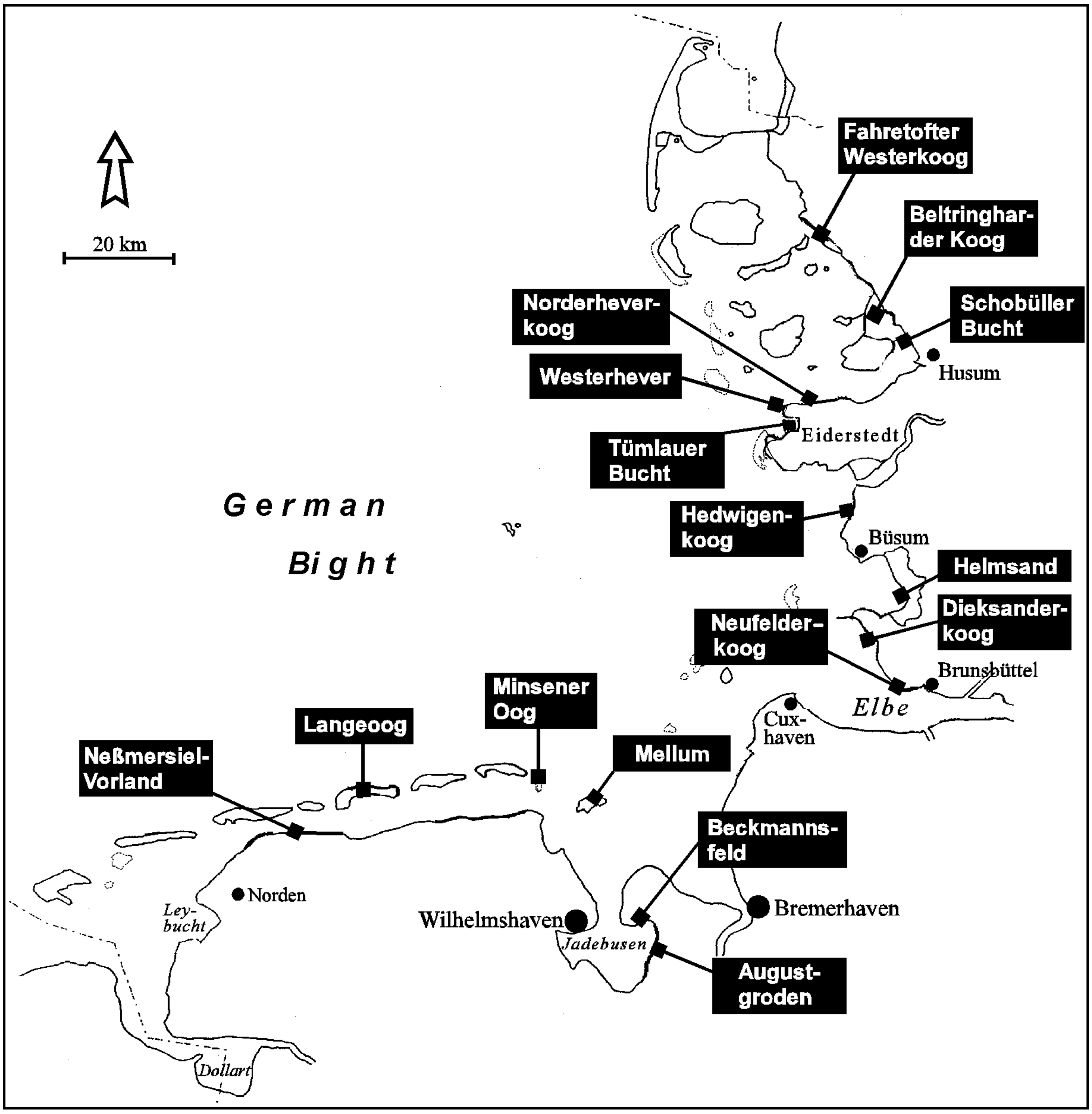

Fig. 5.1: Map of the German Bight and geographical location of the study areas.

Caused by fluctuations in breeding bird numbers, locations of study sites were changed in some cases (Table 5.1). A few times, running examinations could only be carried out insufficiently or had to be stopped. The planned monitoring of Avocets in a large colony at the Leybucht could not be carried out, because there was no colony with characteristics demanded in the methodological instructions (isolated site, 50-100 breeding pairs). Instead of this, an Avocet colony at Augustgroden was observed in 1997 but only hatching success and not breeding success was observed because of the unclear landscape at this location.

Table 5.1: List of species and study areas monitored and description of colony and breeding locations. On areas only described by 'salt marsh', different types of vegetation were settled for breeding. LS = Lower Saxony, SH = Schleswig-Holstein, Jadeb.= Jadebusen, s. m. = salt marsh, part. int. grazed = partial intensively sheep-grazed pastures.

Region (Federal state)	Year	Type of biotope	Cultivation
Herring Gull *Larus argentatus*			
Langeoog-Vogelkolonie (LS)	96/97	Grey dunes	—
Mellum (LS)	96/97	White dunes	—
Black-headed Gull *Larus ridibundus*			
Langeoog-Flinthörn (LS)	96/97	Lower salt marsh	—
Augustgroden/Jadeb. (LS)	96	Lower salt marsh	—
Beckmannsfeld/Jadeb. (LS)	97	Lower salt marsh	—
Westerhever (SH)	96/97	Salt marsh	—
Common Tern *Sterna hirundo*			
Minsener Oog (LS)	96/97	Grey dune/Upper s. m.	—
Augustgroden/Jadeb. (LS)	96	Lower salt marsh	—
Beckmannsfeld/Jadeb. (LS)	97	Lower salt marsh	—
Neufelderkoog (SH)	96	Lower salt marsh	int. grazed
Oystercatcher *Haematopus ostralegus*			
Langeoog-Flinthörn (LS)	96/97	Lower salt marsh	—
Neßmersiel-Vorland (LS)	96	Salt marsh	mainly grazed (partially intensive)
	97		—
Hedwigenkoog (SH)	96/97	Salt marsh	part. int. grazed
Tümlauer Bucht (SH)	96/97	Salt marsh	part. int. grazed
Westerhever (SH)	96/97	Salt marsh	part. int. grazed
Norderheverkoog (SH)	96/97	Lower salt marsh	part. int. grazed
Avocet *Recurvirostra avosetta*			
Augustgroden/Jadeb. (LS)	97	Lower salt marsh	—
Dieksanderkoog (SH)	97	Lower salt marsh	—
Hedwigenkoog (SH)	96	Salt marsh	—
Schobüller Bucht (SH)	96/97	Lower salt marsh	—
Beltringharder Koog (SH)	96/97	No vegetation	—
Fahretoft. Westerkoog (SH)	96/97	No vegetation	—

On Langeoog-Flinthörn, the Black-headed Gulls interrupted setting up a colony in 1997. The building of a suitable alternative colony near the 'Sommerdeich' was interrupted at the advanced breeding season when it was too late to observe a colony on another island. On Langeoog, no further colonies were suited for the monitoring project because they were either influenced by a heavily used footpath, or the topography of the site and the abundance of the birds did not permit an observation according to the guidelines (see 5.3.1.). Hence, only the fates of a few solitary nests were observed at Flinthörn.

At Neufelderkoog, the already started monitoring of the Common Tern colony had to be interrupted because of the urgent resistance of the inhabitants.

Induced by the results reported by Wilkens & Exo (1998), Herring Gulls on Mellum were monitored in a northern and a southern subcolony in 1997.

To test the methodological recommendations beforehand, Black-headed Gulls were monitored at two sites on the mainland of Schleswig-Holstein already in 1995 (Helmsand and Westerhever, see Fig. 5.1). The results of these observations are partly presented as comparative values in the following paragraphs, but they are not subject of any detailed description.

5.3. Methods

5.3.1. Methodological guideline

As mentioned above, the methodological basis of the project was a concept which was developed by an expert group co-operating with the 'National Co-ordinator Group on the Joint Monitoring Program for Breeding Birds in the Wadden Sea' (Exo *et al.* 1996). This guideline provides the survey of hatching and breeding success as well as observing chick development of selected species. The data are supposed to be collected by regular nest inspections during the whole breeding season. According to the species-specific breeding biology, different methods are recommended. Data of parameters of different quality and relevance are supposed to be collected. In case of all species, hatching success is expected to be ascertained. To determine reproductive success of Avocets, it is proposed to conduct censuses of flightless chicks in their feeding and raising territories. In case of gulls and terns, it is recommended to register breeding success and body mass development of chicks at enclosed nest sites.

As a rule, the studies were conducted strictly according to these guidelines. In some cases, the monitoring was part of already established research programs (e.g. Becker 1991). In these cases, nest inspection intervals differ from the recommended ones. This is regarded in the following presentations (see 5.4.) but there were obviously no consequences for the comparableness of the results.

5.3.2. Standardization of analyses

To produce reliable and reproducible results, it was necessary to determine standardised decisive criteria and conventions not only for fieldwork but also for the analyses.

Because dating the time of hatching usually was feasible, conclusions on the fate of a clutch (decision 'hatched' vs. 'not hatched') could mostly be drawn without problems. In contrast, it was more difficult to date the fledging time of a chick. All chicks which were not present in their enclosed area during one nest inspection were assumed to be fledged if they had reached a particular age (e.g. Becker & Finck 1986). In case of Herring Gulls, this key-date was an age of 28 d, in Black-headed Gulls 21 d, and in Common Terns 18 d.

The definitive determination of causes of egg or chick losses was only possible for a more or less big fraction of clutches or families. Experiences show that most predator species leave the nest-site after removing their prey. Therefore, all 'disappeared' not hatched eggs or not fledged larid chicks were arbitrarily classified as 'loss caused by predation' (Table 5.2) although other causes of losses basically were possible, too (for example man-made causes). Further causes of egg or chick losses could be determined by means of specific field observations (Table 5.2). For example, a clutch could be declared as abandoned if eggs

Table 5.2: List of measured and derived parameters presented in this report, their definitions, and their significance as indicators for the following environmental factors: f= food supply, p= pressure by predators, w= weather and climate, t= tide, g= grazing intensity, d= intensity of disturbance by man (e.g. tourism) and predators, e= environmental pollution.

Parameter		Indicating	Definition
measured/observed	derived		
Breeding biology			
Clutch size		f	eggs/clutch ± S.D.
Brood size		p,t,g,d,e	hatched chicks/clutch ± S.D.
Breeding success		f,p,w	fledged chicks/clutch ± S.D.
Fate of offspring			
Condition of eggs:			
Hatched	Hatching success	p,t,g,d,e	hatched chicks in % of all eggs
	Hatching probability P_M	p,g	hatching probability according to Mayfield (1961, 1975) with respect to eggs
	Egg mortality	p,t,g,d,e	non-hatched eggs in % of all eggs, distinguishable according to mortality factors
	Egg mortality factors:		
Disappeared	Predation	p	
Broken	Predation	p	
	Trampling by cattle/sheep	g	
Cold and damp	Abandonment of clutches	p,d	
	Infertility of eggs or dying of embryos	d,e	
Flooded	Flooding	w,t	
Condition of chicks:			
Fledged	Reproductive success	f,p,w,t,g,d,e	fledged chicks in % of all eggs
	Fledging success	f,p,w	fledged chicks in % of hatched chicks
	Nestling mortality	f,p,w	non-fledged chicks in % of all chicks, distinguishable according to mortality factors
	Chick mortality factors:		
Disappeared	Predation	p	
Dead, injured	Predation	p	
Dead, no external injuries	Starvation, hypothermia, or disease	f,w,d	
Flooded	Flooding	w,t	
Body mass development of chicks			
Growth rate of all chicks Gr_a		f,w	average daily increase in weight during the phase of linear growth in g/d ± S.D.
Growth rate of fledged chicks Gr_f		f,w	see above
Maximal body mass		f,w	average max. body mass during the development of fledged chicks in g ± S.D.
Age at maximal body mass		f,w	average age of fledged chicks at maximal body mass in d ± S.D.
Fledging mass		f,w	average body mass of fledged chicks at the last measurement before fledging in g ± S.D.
Fledging age		f,w	average age of fledged chicks at the last inspection before fledging in d ± S.D.

were found cold and damp before the expected hatching date. In contrast, eggs were assumed to be unfertilised or dead if they were found cold and damp after a sufficient time of incubation.

At Neufelderkoog (Common Terns) and at the eastern Jadebusen (Black-headed Gulls) eggs were collected for a monitoring of chemicals in coastal birds (Becker *et al.* 1998). These eggs were excluded from analyses. They rather were handled as not being produced (except for the parameter clutch size). The resulting deviation of breeding success from the potential possible one has to be considered when the results are interpreted.

The successive measurement of the body mass development of the larid chicks was carried out by a mobile electronic balance measuring with a precision of ± 1g (see e.g. Wilkens 1996, Becker *et al.* 1997b). As a comparative value representing the pattern of chick growth, the average daily increase in body mass during the period of approximate linear growth was calculated. Though, particular cases were not reviewed whether the increase in body mass was really a linear one and whether the growth was linear during the whole relevant period, respectively. In Herring Gull nestlings, the phase of approximate linear growth was assumed to occur at the age of 5-25 d, in Black-headed Gulls at an age of 5-15 d, and in Common Terns at the age of 3-13 d (see e.g. Mlody & Becker 1991, Wilkens & Exo 1998). The growth rates are calculated with respect to all chicks (“Gr_a”) and with respect to fledged chicks only (“Gr_f”). The growth curves are related to all chicks staying alive during one interval of nest inspection (see 5.4.4.). For further parameters of chick development see Table 5.2.

The chicks’ ages could only be determined exactly when chicks hatched right during the nest inspection or a short time before this. The designation “age of chicks” means “age class” in the following chapters. For example, age class 1: chicks of an age of 0 (= day of hatching) to 1 day (in case of a nest inspection interval of two days) and chicks of an age of 0 to 2 days (in case of an inspection interval of three days), respectively.

5.3.3. Parameters of breeding success; Statistics

Several different parameters were measured to analyse breeding success and breeding performance of the birds. Further parameters could be derived by particular calculations or by applying the standardisations elucidated in 5.3.2. For the significance as indicators for environmental factors and definitions of these parameters see Table 5.2.

In case of the observed waders, the hatching probabilities of eggs according to Mayfield (1961, 1975) were calculated. In contrast to the ‘relative hatching success’, which is based on the number of found and observed eggs, the value of hatching probability of eggs is based on the duration of egg survival (‘egg-days’, see Table 5.2). Especially in cases in which eggs are lost before they are found, e.g. at sites with a high predation pressure, hatching probabilities of eggs represent the ‘true hatching success’ of the birds more realistically than observed percentages of hatched chicks.

The average incubation period of successfully incubated Avocet eggs was considered to last 25 d (Glutz von Blotzheim & Bauer 1986), that of Oystercatchers 26 d (Glutz von Blotzheim *et al.* 1999). For calculating the egg-days of lost eggs, the dates of losses have to be determined. In case of presumably predated eggs, losses were assumed to have taken place midway between the two last inspections. In case of dead or abandoned eggs, losses are assumed to have occurred at the inspection date that follows the expected hatching date.

Most features are indicative of more than one environmental factor (Table 5.2). To use the parameters of breeding success as indicators for environmental changes, single parameters should not be looked at out of the context. For example, the value ‘breeding success’ is important to evaluate future development of breeding bird populations and, thus, to assess the necessity of particular protection measures (see introduction and discussion). Therefore, conclusions concerning environmental influences on breeding success can only be drawn by analysing supplementary parameters such as mortality factors and growth rates of chicks. Through the analysis of a multitude of parameters measured and observed by monitoring breeding success, environmental influences as well as their effects on breeding birds can be defined (see discussion).

Statistics were performed according to Sachs (1997). Only non-parametric two-tailed tests were applied. Levels of significance were symbolised in the following way: n.s.= not significant, * = ($p<0.05$), **= ($p<0.01$), ***=($p<0.001$). Standard deviations are abbreviated to S.D.

5.4. Results

5.4.1. Hatching success and causes of egg losses

Larids

The larids’ hatching success and causes of egg losses varied interspecifically as well as intraspecifically according to colony site and breeding season (Fig. 5.2).

Herring Gulls achieved high success in general, and hatching success varied only slightly between 1996 and 1997 and between the colony sites on Langeoog and on Mellum. Neither different hatching success nor different spectra of causes of egg losses were found (χ^2-test, n.s.). Most frequent and nearly single causes of unsuccessful incubation were unfertilised eggs and dead embryos (ca. 3-15 %). In this species, egg predation was unimportant.

In contrast, all eggs of Black-headed Gulls breeding on Langeoog were predated in both study years (in 1996 probably by small mammals like Hedgehogs *Erinaceus europaeus* and rats *Rattus* spec.; in 1997 possibly by Herring Gulls). The birds breeding at the eastern Jadebusen and at Westerhever incubated more successful. Their hatching success was significantly higher in 1996 than in 1997 (χ^2= 4.72 and 11.25, d.f.= 1, $p<0.05$ and $p<0.001$; Thus, hatching success achieved in 1997 was comparable to the values of Helmsand and Westerhever in 1995 which were about 80.4 % and 85.3 %). At both sites, a decrease in predation was observed (Jadebusen: χ^2= 28.37, d.f.= 4, $p<0.001$; Westerhever: χ^2= 15.35, d.f.= 3, $p<0.01$). In 1997, the gulls achieved lower success at the eastern Jadebusen than at Westerhever because of flooding and unfertilised eggs (χ^2= 4.87, d.f.= 1, $p<0.05$).

Similar to some Black-headed Gull colonies, Common Terns suffered total egg losses caused by predation at Augustgroden in 1996. In 1997, corresponding losses were less

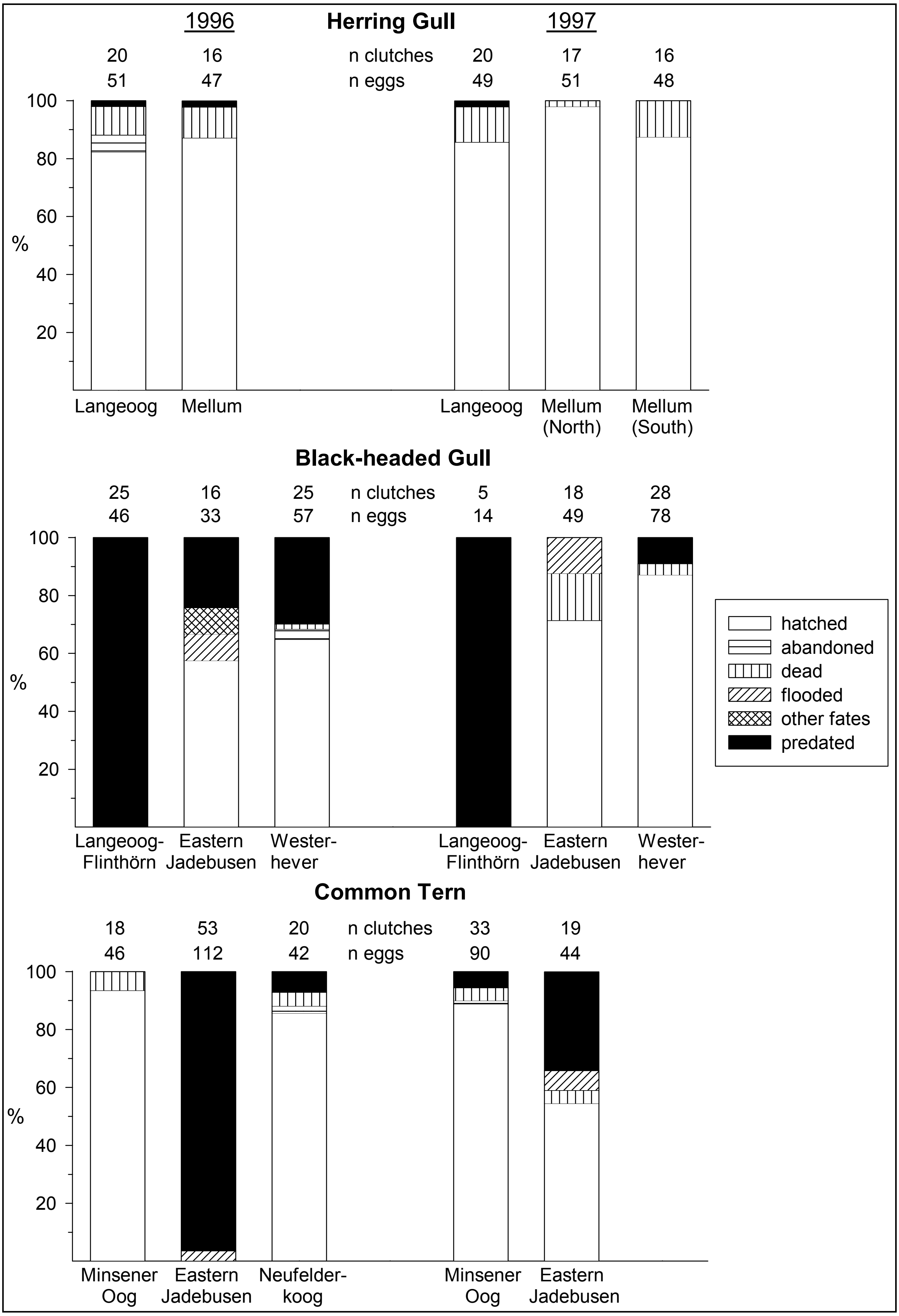

Fig. 5.2: Hatching success and fate of not hatched eggs (in % of Σ eggs each) of larid species at different colony sites in 1996 and 1997. At Neufelderkoog and at the Jadebusen (Black-headed Gull), eggs were removed for monitoring chemicals. These eggs were excluded from analyses.

frequent (χ^2= 82.49, d.f.= 3, p<0.001) but again a large part of eggs fell victim to predators (see below). Accordingly, the terns were less successful at the Jadebusen than on Minsener Oog in both years (1997: χ^2= 20.06, d.f.= 1, p<0.001) and than at Neufelderkoog in 1996. In contrast, the birds of Minsener Oog (1996 and 1997) and Neufelderkoog nearly had identical hatching success, different frequencies of causes of egg losses were not found, either.

According to observations of the fieldworkers in 1996, Red Foxes (*Vulpes vulpes*) were the main egg predators at the Jadebusen as well as at Westerhever. At Westerhever, martens (*Mustelidae*) were observed additionally. In nearly all regions, gulls (*L. argentatus, L. canus, L. ridibundus*) and crows (*Corvidae*) occurred.

Oystercatchers

Hatching success of Oystercatchers varied between years and between breeding places (Fig. 5.3). The probabilities that eggs survived the incubation period were mostly higher in 1997 than in 1996. A reverse tendency was only found in case of the breeding pairs of the foreland of Neßmersiel.

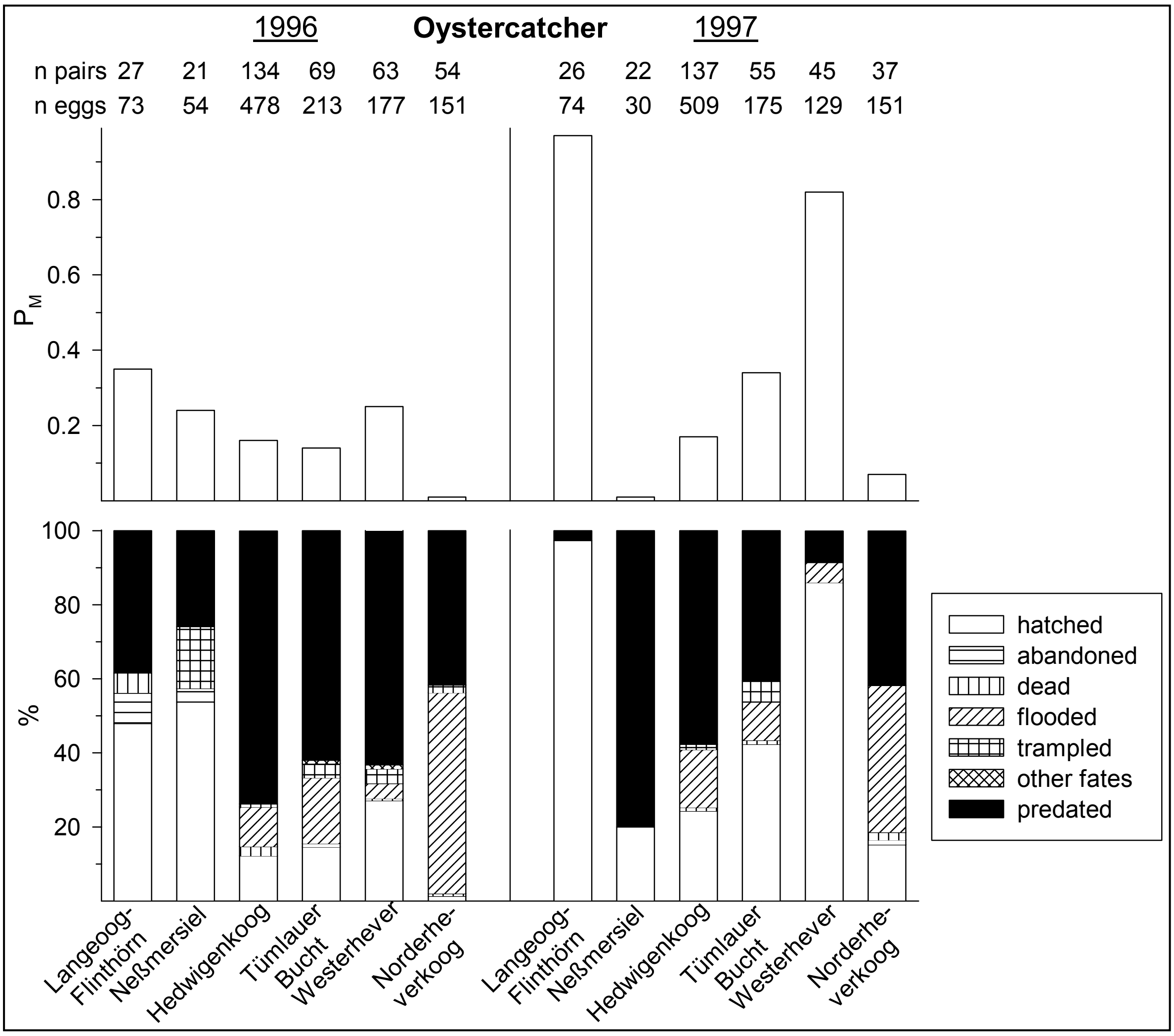

Fig. 5.3: Hatching success and presumed fate of eggs of Oystercatchers at different breeding places in 1996 and 1997. The upper graph represents hatching probabilities with respect to eggs (P_M) according to Mayfield (1961, 1975), the lower one represents the fate of eggs in % of all eggs.

At all locations, a decrease in predation but relative constant frequencies of egg losses caused by other fates were revealed in 1997 (χ^2-tests, $p<0.001$ each). Again, exceptions were found at Neßmersiel where a reverse tendency occurred, and at Norderheverkoog, where losses caused by predation were constant between years, but frequencies of flooded eggs were lower in 1997.

The spectra of presumed causes of egg losses varied between regions (1996: χ^2= 475.61, d.f.= 30, $p<0.001$; 1997: χ^2= 417.89, d.f.= 25, $p<0.001$). Except for Norderheverkoog, the most important cause was predation. On the mainland, foxes should have been more or less important predators. Egg losses caused by flooding were registered exclusively in Schleswig-Holstein. Trampling by sheep was a regular cause of losses especially in Schleswig-Holstein, but only in a few cases (e.g. Tümlauer Bucht in 1997) these losses were considerable ones. Remarkable is the high frequency of eggs lost by cattle trampling at Neßmersiel in 1996.

Table 5.3: Hatching success of Oystercatchers breeding on pastures and uncultivated land in 1996 and 1997 (see also 5.2. and 5.5.1.). HS= hatching success in % of all eggs, P_M= hatching probability according to Mayfield (1961, 1975).

	1996				1997			
	Uncultivated land		Pasture		Uncultivated land		Pasture	
	HS	P_M	HS	P_M	HS	P_M	HS	P_M
Neßmersiel	60.0	0.96	48.3	0.92				
Hedwigenkoog	8.6	0.93	23.2	0.94	27.8	0.94	17.8	0.91
Tümlauer Bucht	15.5	0.93	13.4	0.93	50.0	0.96	34.8	0.96
Westerhever	25.0	0.94	30.4	0.96	88.5	1.00	84.4	0.99
Norderheverkoog	0.8	0.84	5.3	0.88	23.0	0.91	4.7	0.90

In most cases, Oystercatchers achieved higher hatching success on uncultivated areas than on pastures. But in Schleswig-Holstein, ratios of hatching success achieved on different pieces of agriculturally used land were often inverse (Table 5.3): Especially on plots of the foreland which were not grazed to its outer edge and where large frequencies of egg losses caused by predation and flooding occurred (e.g. at Hedwigenkoog and at Norderheverkoog in 1996), hatching success was higher on pastures than on uncultivated land (Fig. 5.3, see 5.5.1.). In contrast to pasture grazed at low intensity (0.5 cattle/ha; see Table 5.3), the birds achieved no hatching success on pieces of intensively grazed land (2.2 cattle/ha) at Neßmersiel.

Avocets

Similar to the Oystercatcher, the Avocet achieved higher hatching probabilities in 1997 than in 1996 at all colony sites observed over two years (Fig. 5.4). At Beltringharder Koog and at Fahretofter Westerkoog, this variation was accompanied again by a decrease in frequencies of presumably predated eggs (χ^2= 141.34, d.f.= 5. $p<0.001$ and χ^2= 82.35, d.f.= 4, $p<0.001$, respectively). Except for the predator species mentioned above, again foxes played the most important role for the large frequencies of lost eggs particularly at Beltringharder Koog.

In case of Oystercatchers as well as in case of Avocets, close correlations (according to Spearman) between the relative hatching success and the hatching probabilities were found: Oystercatcher r_S= 0.88, n= 12, p<0.001; Avocet r_S= 0.99, n= 9, p<0.001.

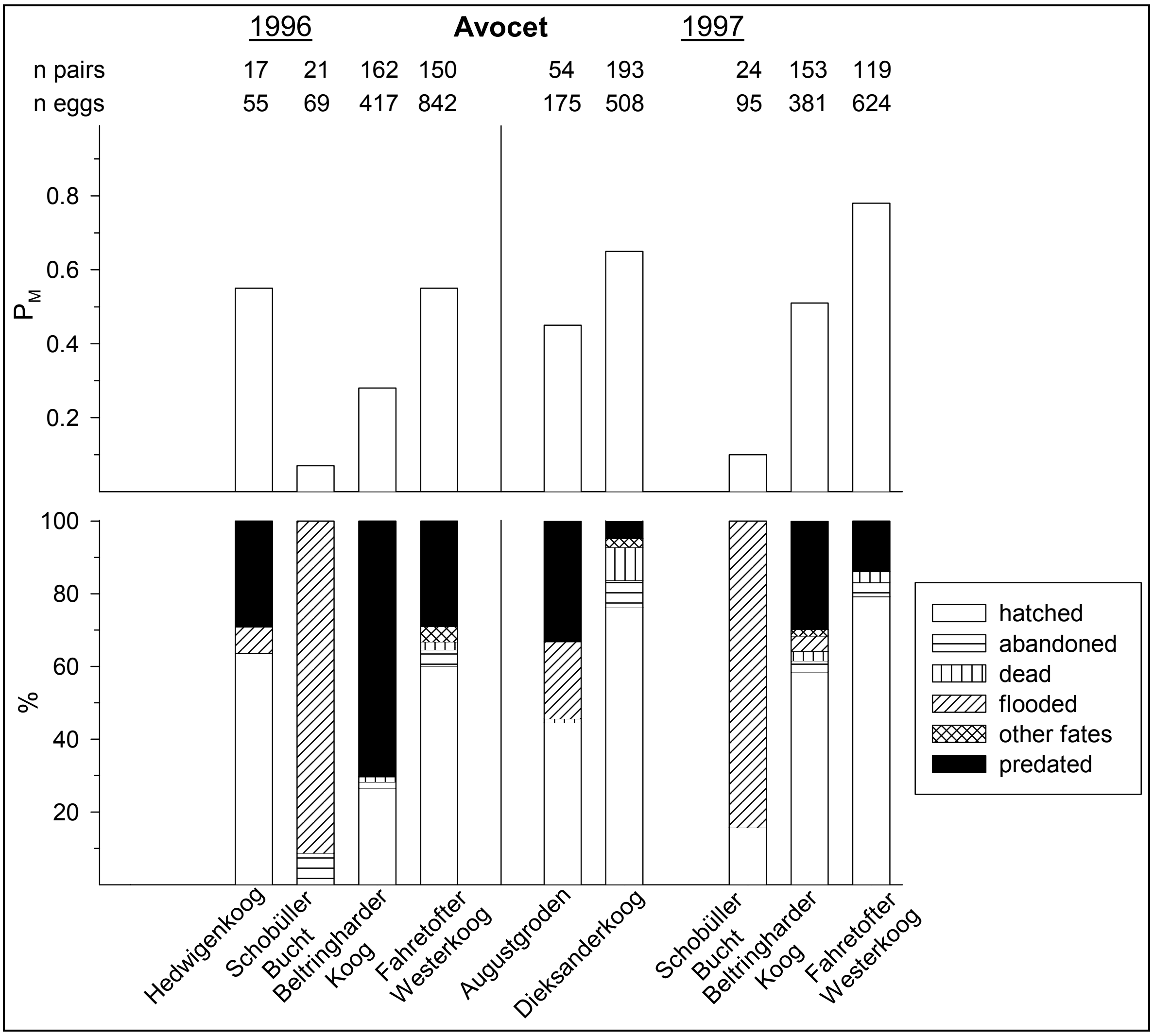

Fig. 5.4: Hatching success and presumed fate of eggs of Avocets at different colony sites in 1996 and 1997. The upper graph represents hatching probabilities with respect to eggs (P_M) according to Mayfield (1961, 1975), the lower one represents the fate of eggs in % of all eggs.

5.4.2. Reproductive and breeding success

Larids

Similar to hatching success, reproductive success of Herring Gulls did not differ between colony sites and years (χ^2-test, n.s.; Fig. 5.5). Only in 1997, the reproductive outputs differ between the southern subcolony of Mellum and the colony of Langeoog (Nemenyi test p<0.05).

In comparison, relatively high variations in reproductive and breeding success were found in Black-headed Gulls. At Westerhever, more chicks fledged in 1997 than in 1996 (χ^2= 34.98, d.f.= 1, p<0.001 and Nemenyi test p<0.001), whereas the number of fledged young was constant between years at the Jadebusen. In 1996, the gulls of the Jadebusen bred more successful, in 1997, the pairs of Westerhever (χ^2= 8.21, d.f.= 1, p<0.01 and χ^2= 9.15, d.f.=1, p<0.01). However, intersite differences in the reproductive output were only found in 1997 (p<0.05).

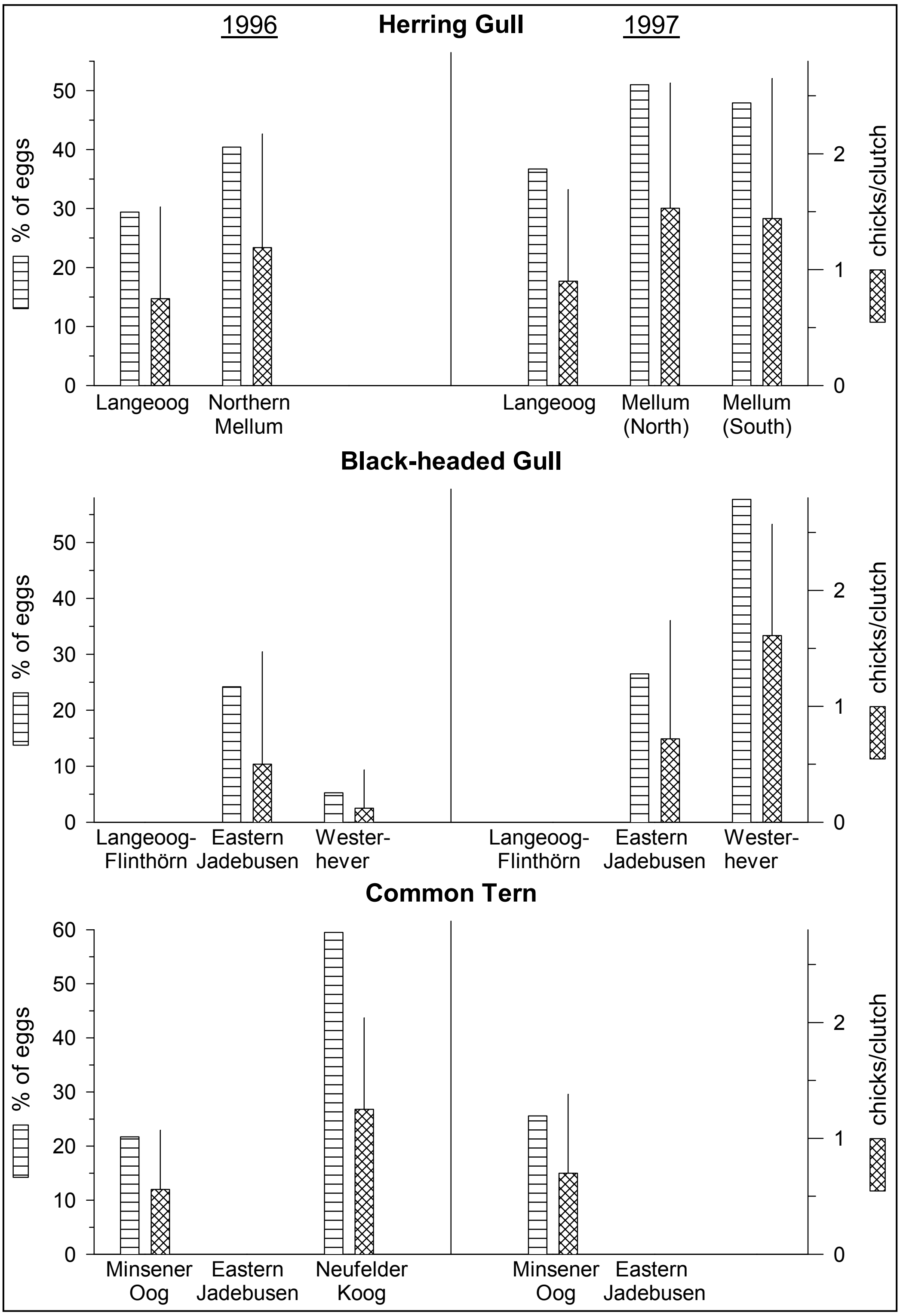

Fig. 5.5: Reproductive (in % of all eggs) and breeding success (average number of fledged chicks/clutch ± S.D.) of larids at different colony sites in 1996 and 1997. At Neufelderkoog and at the Jadebusen (Black-headed Gull), eggs were removed for monitoring chemicals. These eggs were excluded from analyses.

Both in 1996 and 1997, the Common Terns of the Jadebusen did not have any breeding success. The terns on Minsener Oog bred more successfully but without any variation, too: Their reproductive success as well as their breeding success had nearly identical values in both years. Highest success and the largest output was achieved by the terns of Neufelderkoog in 1996: In this colony, the values of both parameters were significantly higher than on Minsener Oog (χ^2= 13.09, d.f.= 1, p<0.001; Nemenyi test p<0.05).

Avocet

Avocets reproduced obviously less successfully than gulls and terns in general (Fig. 5.6, Fig. 5.5). At only two colony sites, the birds bred without total losses, but with very low success in 1996.

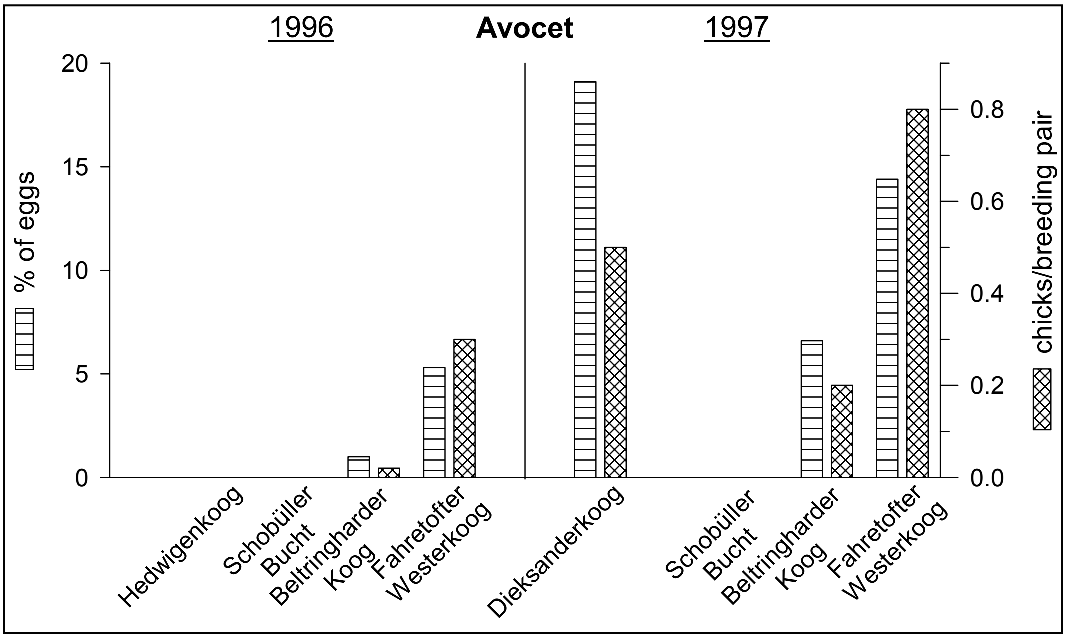

Fig. 5.6: Reproductive (in % of all eggs) and average breeding success (Σ fledged chicks/Σ breeding pairs) of Avocets at different colony sites in Schleswig-Holstein in 1996 and 1997.

At places observed during both study years, the breeding pairs were much more successful in 1997 than in 1996 (χ^2= 17.84 and 34.98, d.f.= 1, p<0.001 each). In both years, Avocets achieved higher success at Fahretofter Westerkoog than at Beltringharder Koog (χ^2= 14.4 each, d.f.= 1, p<0.001 each).

5.4.3. Chick mortality and causes of chick losses

Fate of the nestlings

According to age, colony site, and breeding season, the observed chicks survived their rearing periods with different frequencies (Fig. 5.7).

In case of the Herring Gulls breeding on Langeoog, relatively fewer chicks were found dead in 1997 than in 1996 (i.e. chicks whose death was not caused by one of the factors listed in Fig. 5.7). Although young fell victim to predators more often in 1997, more chicks proportionally survived and fledged in that year (χ^2= 6.66, d.f.= 2, p<0.05).

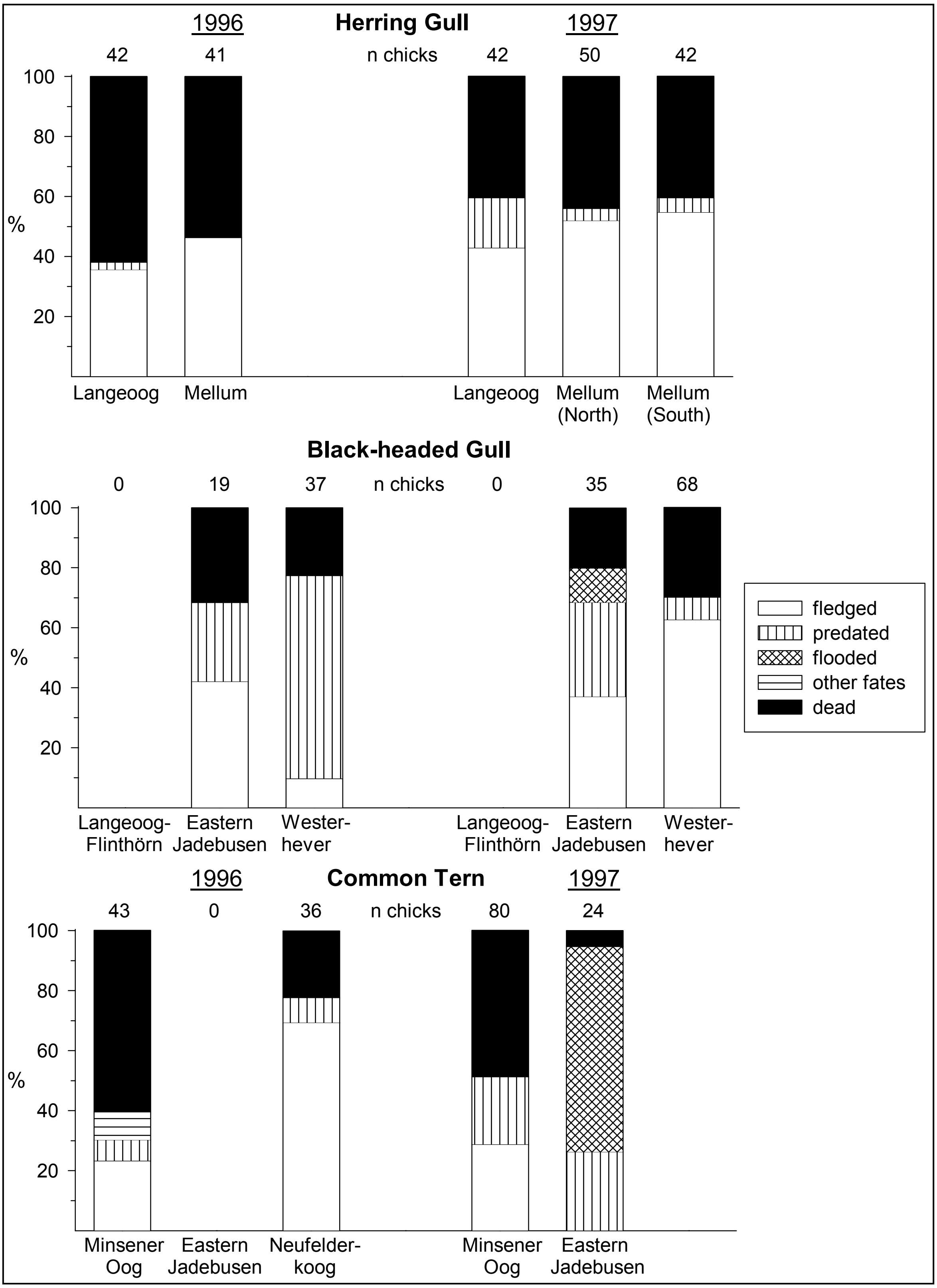

Fig. 5.7: Frequencies of various fates of chicks of three larid species breeding at different colony sites in 1996 and 1997.

On Mellum, predation was higher in 1997, but neither frequencies of chicks found dead nor the number of chicks surviving varied significantly between years. Intersite differences in fate of chicks were not found in both years of study.

Black-headed Gull chicks hatched at the Jadebusen in 1996 and 1997 fledged with comparable frequencies. The spectra of observed fates did not differ significantly. In contrast, only a few of the young fledged at Westerhever in 1996 but they did for the most part in 1997. (In comparison, fledging success at Westerhever in 1995: 46.5 %, at Helmsand: 72.5 %). In 1996, fledging success obviously was not restricted by a bad chick vitality, but by a large frequency of predated chicks which was significantly lower in 1997 (χ^2= 42.4, d.f.= 2, $p<0.001$). Corresponding to this observation, more chicks fledged at the eastern Jadebusen than at Westerhever in 1996 (χ^2= 19.61, d.f.= 2, $p<0.001$), whereas this ratio was inverse in 1997 (χ^2= 19.7, d.f.= 3, $p<0.001$).

As mentioned above, the Common Terns of the Jadebusen suffered total breeding failures in 1996 as well as in 1997. In 1996, even no hatching success was achieved, whereas in 1997, offspring died during chick rearing by flooding and predation. At the other sites, the breeding pairs produced fledged young. On Minsener Oog, where the frequencies of fledged chicks differed slightly between years (χ^2= 22.3, d.f.= 3, $p<0.01$), fledging success of the terns was lower than at Neufelderkoog in 1996 (χ^2= 19.49, d.f.= 3, $p<0.001$). The birds of the latter site raised their young very successfully.

All species mentioned in paragraph 5.4.1. are possible chick predators, too. At all mainland sites presented in Fig. 5.7, foxes were responsible for large chick losses especially at Westerhever in 1996. Marsh Harriers (*Circus aeruginosus*) were further potential predators. Moreover, Short-eared Owls (*Asio flammeus*) and Northern Harriers (*Circus cyaneus*) were observed regularly on the islands.

Chick mortality dependent on age

In some cases, frequencies of nestlings found dead depended on different stages of chick development (Fig. 5.8). This is applicable, especially, in case of the young Herring Gulls on Langeoog. In contrast, on Mellum dead chicks were found with uniform frequencies during the rearing period.

On Langeoog, chicks died more frequently in the first days of their life in 1996 than in 1997, whereas mortality of ten- to twenty-day-old chicks was similar in both years. In both seasons, approximately 70 % of chicks hatched at third, and 30 % of chicks hatched at second position, did not survive the first three weeks after hatching. In the ensuing rearing stages, chick mortality was lower in 1997 than in 1996.

In contrast to the offspring of the Jadebusen in 1997 and of Westerhever in 1996, Black-headed Gull nestlings at the Jadebusen did not die in the first days of their life in 1996 but, mainly, at an age of two to three weeks. In 1997, fewer ‘first’ and ‘second’ nestlings, but more frequent ‘third’ chicks (which did not occur in 1996) died during that life stage. At Westerhever, all perished chicks were recorded a short time after hatching in 1996. In contrast, chick mortality was lower altogether in 1997 and, obviously, an age-dependent chick mortality in that season did not exist. On Minsener Oog, most Common Tern chicks died during the first ten days of chick rearing in 1996 as well as in 1997. In both years, the mortality during this period amounted to nearly 90 % of chicks hatched at third position. In contrast to 1996, the findings were restricted nearly exclusively to chicks of an age mentioned above in 1997, whereas all older chicks survived except for a few cases. At Neufelderkoog, chick mortality was low in general. Chicks younger than ten days mainly were affected.

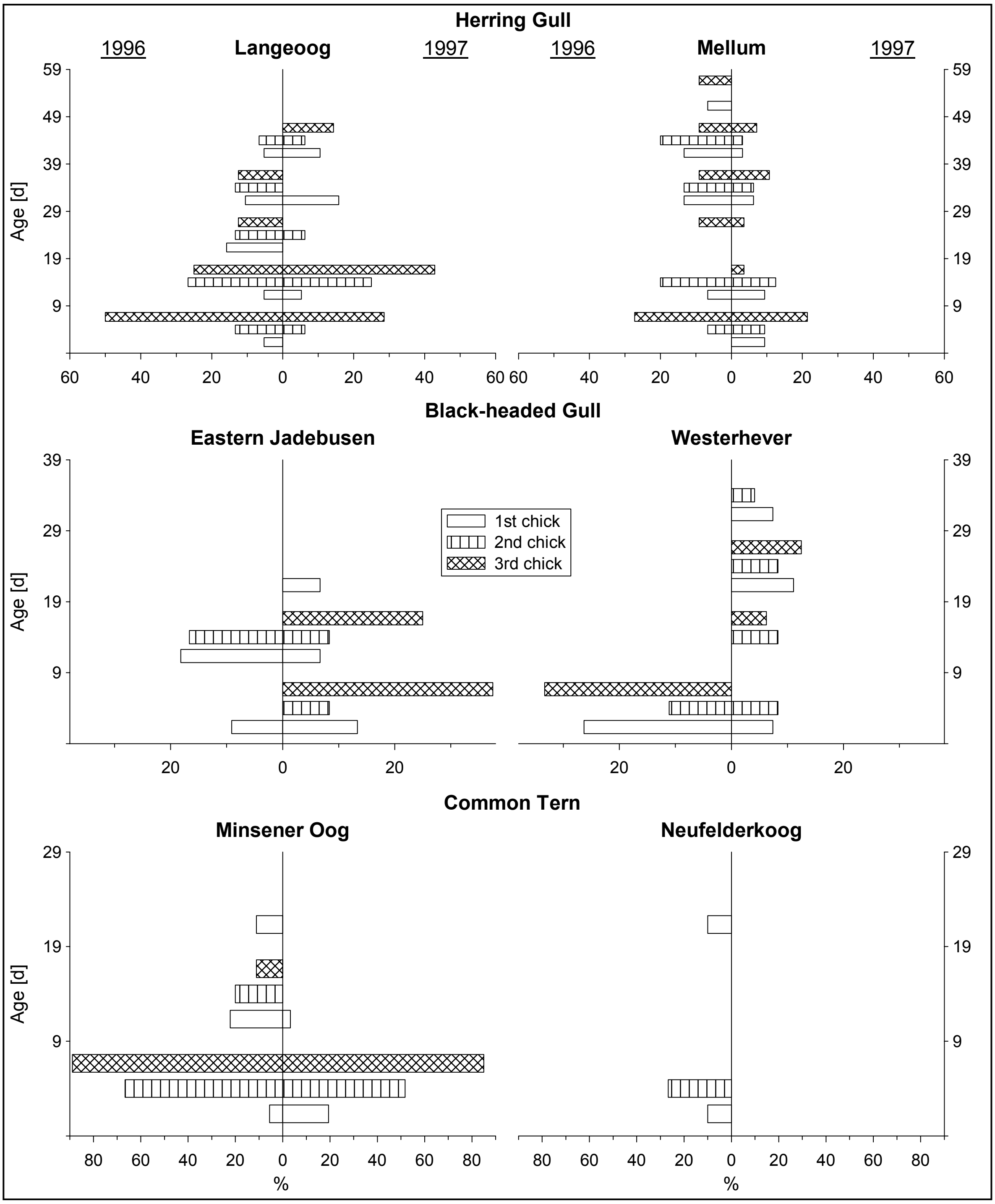

Fig. 5.8: Frequencies of chicks found dead dependent on age and hatching sequence. At the Jadebusen (Black-headed Gull) and at Neufelderkoog chicks of hatching position 3 are missing because eggs were removed from some nests for monitoring chemicals.

Temporal variation in chick mortality

At both colony sites studied, but especially on Langeoog, a large part of Herring Gull chicks were already found dead at the beginning of the chick raising period in both study years (Fig. 5.9). Most of these were chicks which hatched at second and third position of the hatching sequence. Regarding the chronological distribution of further findings, remarkable differences between Langeoog and Mellum were determined. On the latter, the frequencies of chicks found dead did not vary during the period of raising. Moreover, chick mortality evidently did not depend on hatching sequence. In contrast, numerous dead chicks were found at certain stages of the season on Langeoog. Incidentally, it has to be considered that chicks on Langeoog hatched about one or two weeks later than those on Mellum. In both years, up to 60 % of 'third', and up to 25 % of 'second' chicks, died in the last third of June. Additionally, in 1996, many dead chicks were found in the first third of July, including siblings of hatching position three.

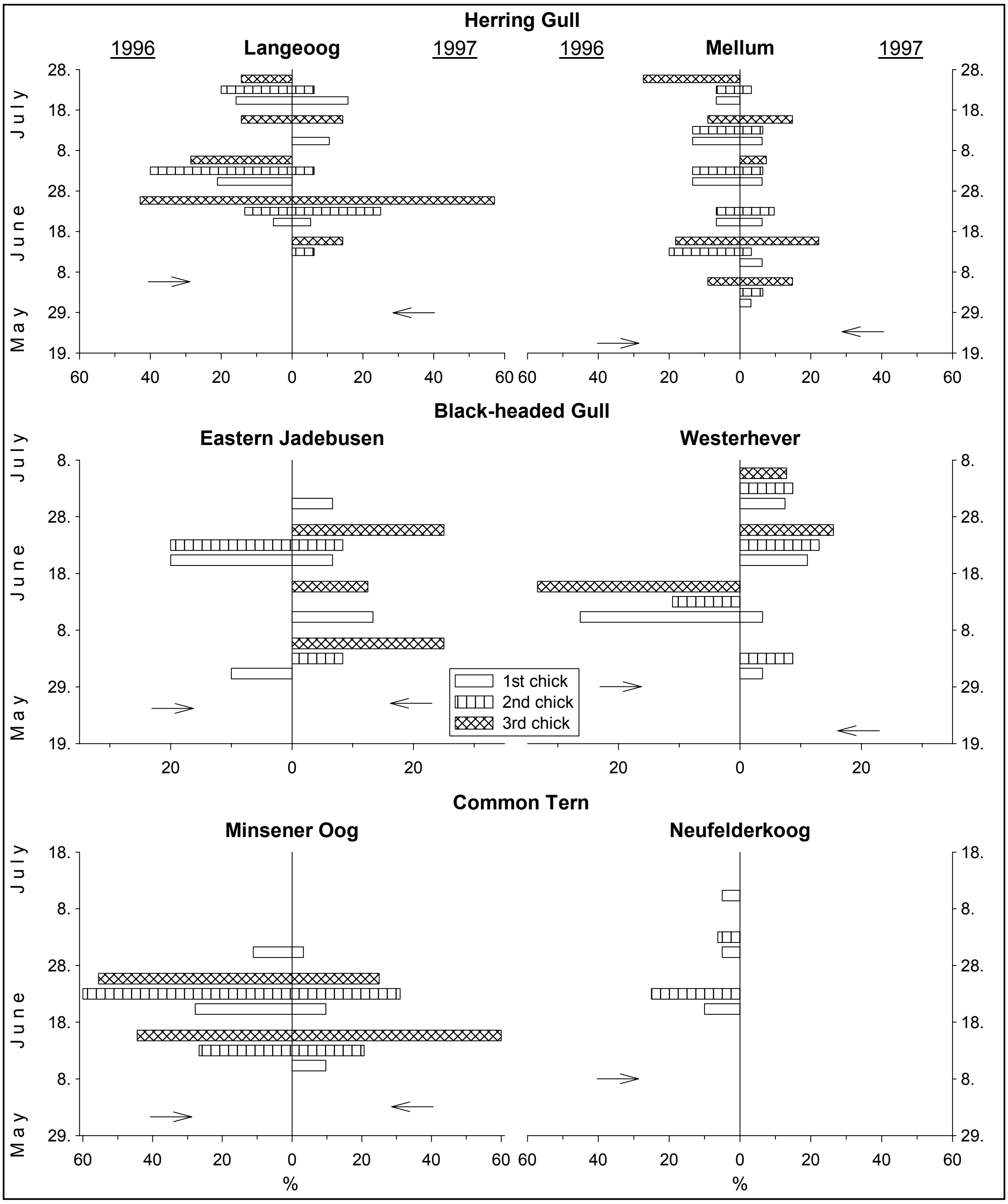

Fig. 5.9: Frequencies of nestlings found dead during different stages of the breeding season. → = average date of hatching of first chicks. At the Jadebusen (Black-headed Gull) and at Neufelderkoog, chicks of hatching position 3 are missing because eggs were removed from some nests for monitoring chemicals.

In the Black-headed Gull colony at the Jadebusen, perished chicks were mostly found at an advanced stage of breeding season towards the end of June in 1996. In comparison, all perished chicks in Westerhever in 1996, were found about ten days earlier. Besides ‘third’ and ‘second’ chicks, considerable numbers of dead chicks hatched at first position were found. Furthermore, in 1997 some concurrent results concerning the season-dependent Black-headed Gull chick mortality were ascertained: Except for some ‘third’ chicks found dead at the beginning of the season, nestlings were found dead, for the most part, at the end of June at the Jadebusen as well as at Westerhever.

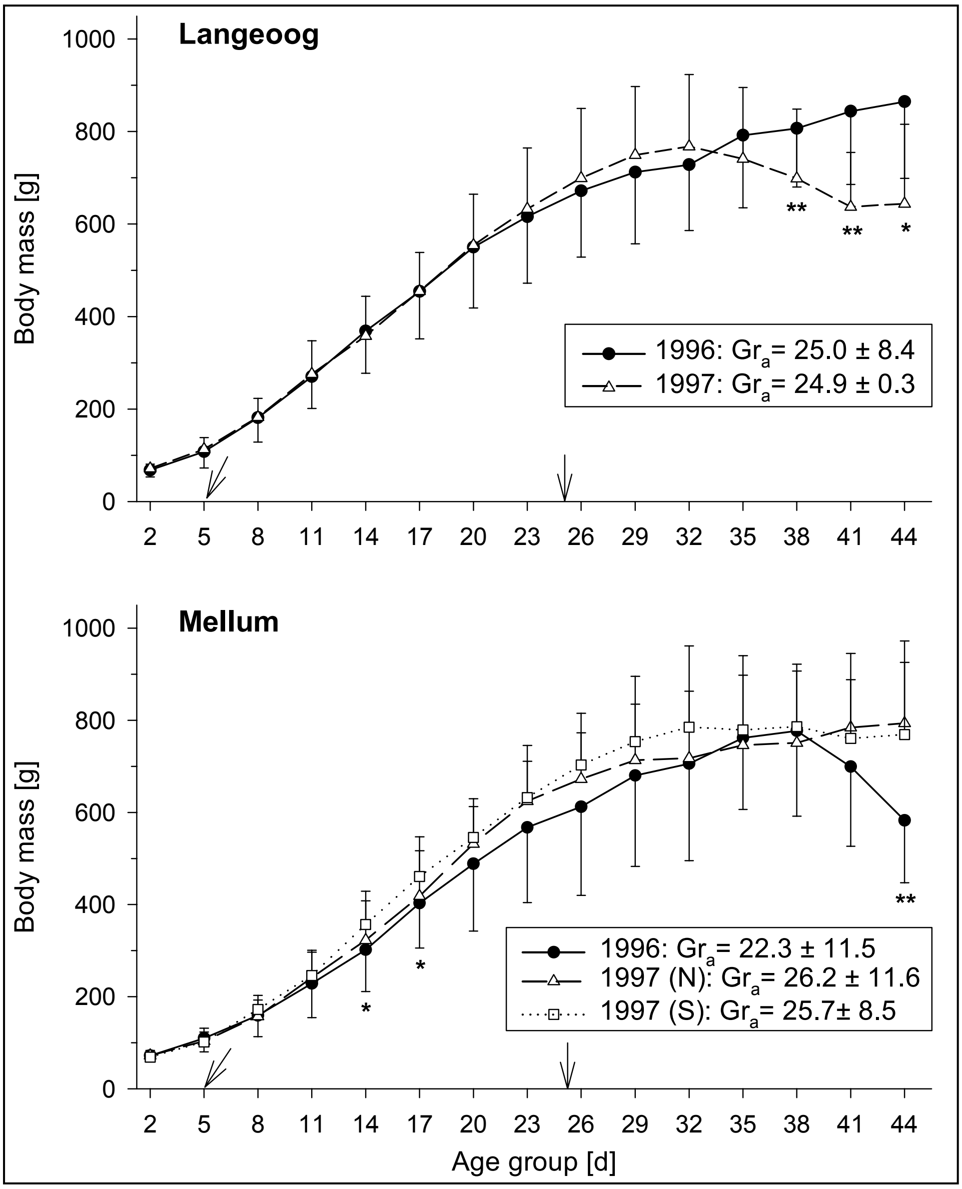

Fig. 5.10: Body mass development of Herring Gull chicks at different colony sites in 1996 and 1997. Given are mean masses of each age group ± S.D. and mean growth rates with regard to all chicks during the stage of linear growth (Gr_a in g/d ± S.D.). ↓ represent empirical limits of the phase of linear growth, (N) = northern subcolony of Mellum, (S) = southern subcolony of Mellum. Age groups with n < 5 chicks (chicks older than 44 d) are excluded from presentation. Significance levels according to U-tests and K-W-tests.

In comparison to some gull colonies, the last decade of June 1996 was important for the mortality of Common Terns chicks as well. On Minsener Oog as well as at Neufelderkoog, dead chicks of all hatching positions were mostly found during this period. In addition, a large number of chicks died during an early stage of development in the middle of June in 1996 and 1997 on Minsener Oog.

5.4.4. Body mass development of chicks

Herring Gull

On Langeoog and Mellum, body masses of Herring Gull nestlings increased with similar rates during the phases of linear growth. The average linear growth rates with regard to all chicks (Gr_a) were about 25 g/d. They differed only slightly and not significantly between years and sites (Nemenyi test; Fig. 5.10). Up to an age of 35 d (Langeoog) and 38 d (Mellum), respectively, the chicks grew in a similar way in 1996 and 1997 (for exceptions see Fig. 5.10).

Considerable differences in the mean age-dependent body masses only occurred in the stage of asymptotic growth a few days before fledging (Langeoog: U-test $p<0.05$, Mellum: K-W-test $p<0.01$). In 1996, the typical recession of body mass during the pre-fledging stage of larid young was not ascertained on Langeoog but, in contrast, a considerable one was found on Mellum.

The mean values of the body masses measured at the last nest inspection before fledging (‘fledging masses’) varied not between years and sites. On Langeoog, these masses were about 858.4 ± 130.3 g (1996) and 728.7 ± 127.6 g, respectively. On Mellum, the fledging masses were between 823.7 ± 105.7 g (northern Mellum in 1997) and 836.0 ± 135.2 g (southern Mellum in 1997). On Langeoog as well as in the southern subcolony of Mellum, the nestlings fledged at an age of 40 d, whereas fledglings were older at the northern site on Mellum (46 ± 7 and 47± 5 d, respectively; Nemenyi test, $p<0.01$ each).

Black-headed Gull

In comparison to 1997, the development of the Black-headed Gull offspring was considerably retarded in 1996, especially at the Jadebusen (Fig. 5.11). At the Jadebusen, the mean daily increase in body mass of the nestlings during the stage of linear growth was higher in 1997 than in 1996 (Nemenyi test $p<0.01$). In contrast, no differences in the linear growth rates were found between the two study years at Westerhever (possibly caused by small sample sizes in 1996).

In 1996, the growth of the five- to fifteen-day-old chicks was not really a linear one at both sites. At the Jadebusen, the body masses of chicks older than nine days were generally lower in 1996 than those of the following year (U-test, see Fig. 5.11). At Westerhever, corresponding differences in age-dependent body masses were already observed in new-hatched chicks.

Despite these interyear differences in the courses of development, the fledging masses did not differ in a significant way between years (Nemenyi test) although the values seem to indicate varying weights. At the Jadebusen, these masses were about 210.3 ± 42.3 g in 1996 and 250.9 ± 25.5 g in 1997, at Westerhever 230.7 ± 26.1 and 244.5 ± 32.2 g, respectively. In 1996, the young fledged at an average age of 22 d in each colony. Thus, fledging age was lower in 1996 than in 1997 (26 ± 2 (Jadebusen) and 28 ± 3 d (Westerhever), respectively; Nemenyi test p<0.001).

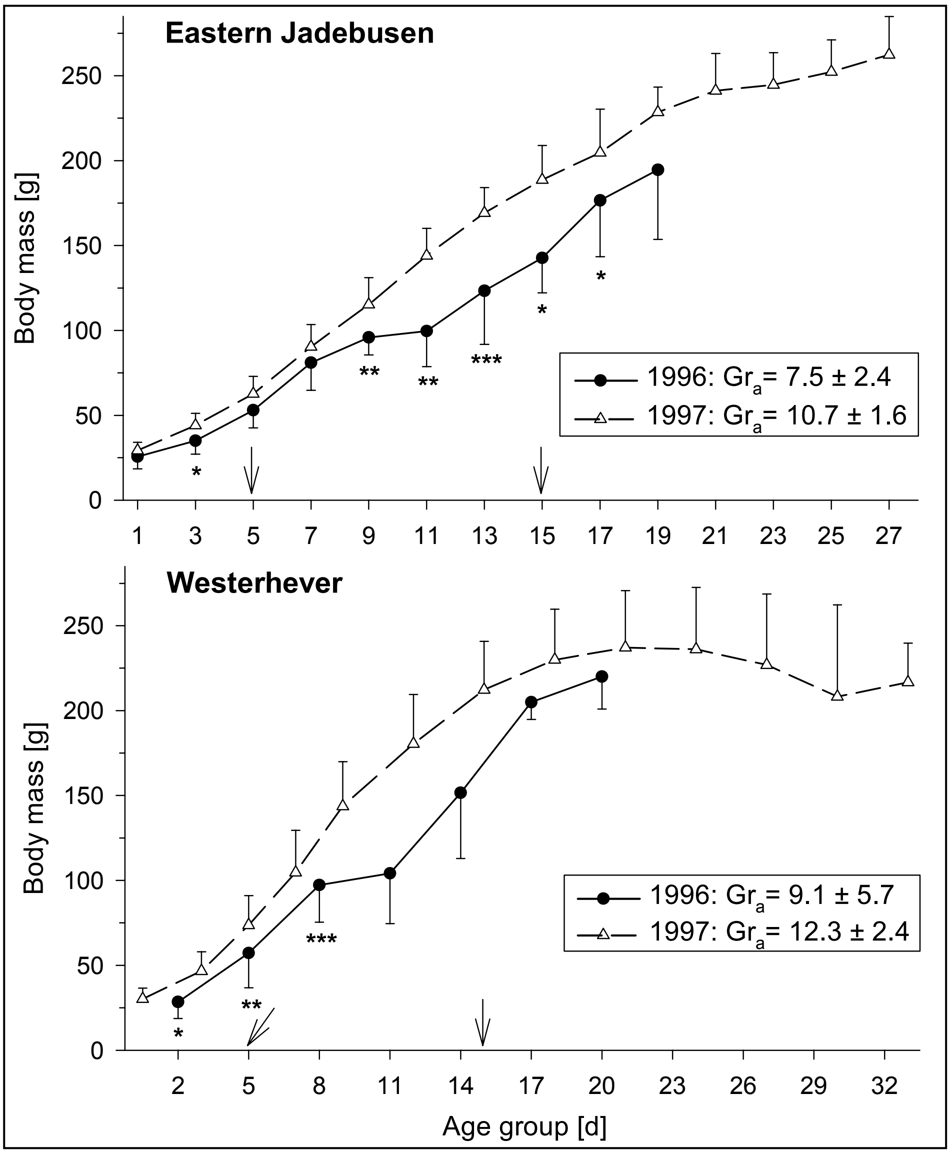

Fig. 5.11: Body mass development of Black-headed Gull chicks at different colony sites in 1996 and 1997. For legend see Fig. 5.10. Age groups with n < 3 chicks are excluded from presentation. Significance levels according to U-tests. Note the different scalings of x-axes.

Common Tern

In 1996 as well as in 1997, the tern chicks grew with a higher rate at Neufelderkoog than on Minsener Oog (Nemenyi test, p<0.001 each). On Minsener Oog, the growth rates did not differ between years. At this site, the growth patterns did not vary until the end of the stage of linear growth. But at an age of 13 d to 25 d, the nestlings weighed generally less in 1996 than in 1997 (U-test; see Fig. 5.12).

Although the fledging masses of the young Common Terns were tending towards higher values in 1997 in comparison to 1996, no significant interyear and intersite variations of fledging masses were proved similar to the other examined species (Minsener Oog in 1996: 115.5 ± 16.1 g, 1997: 123.4 ± 6.3 g; Neufelderkoog: 122.6 ± 1.6 g). But again, differing fledging ages occurred. In 1996, the chicks fledged at an age of 22 ± 2 d at Neufelderkoog.

In contrast, the chicks on Minsener Oog fledged at a more advanced age in both years, i.e. 27 ± 1 d and 26 ± 3 d, respectively (Nemenyi test, $p<0.001$ each).

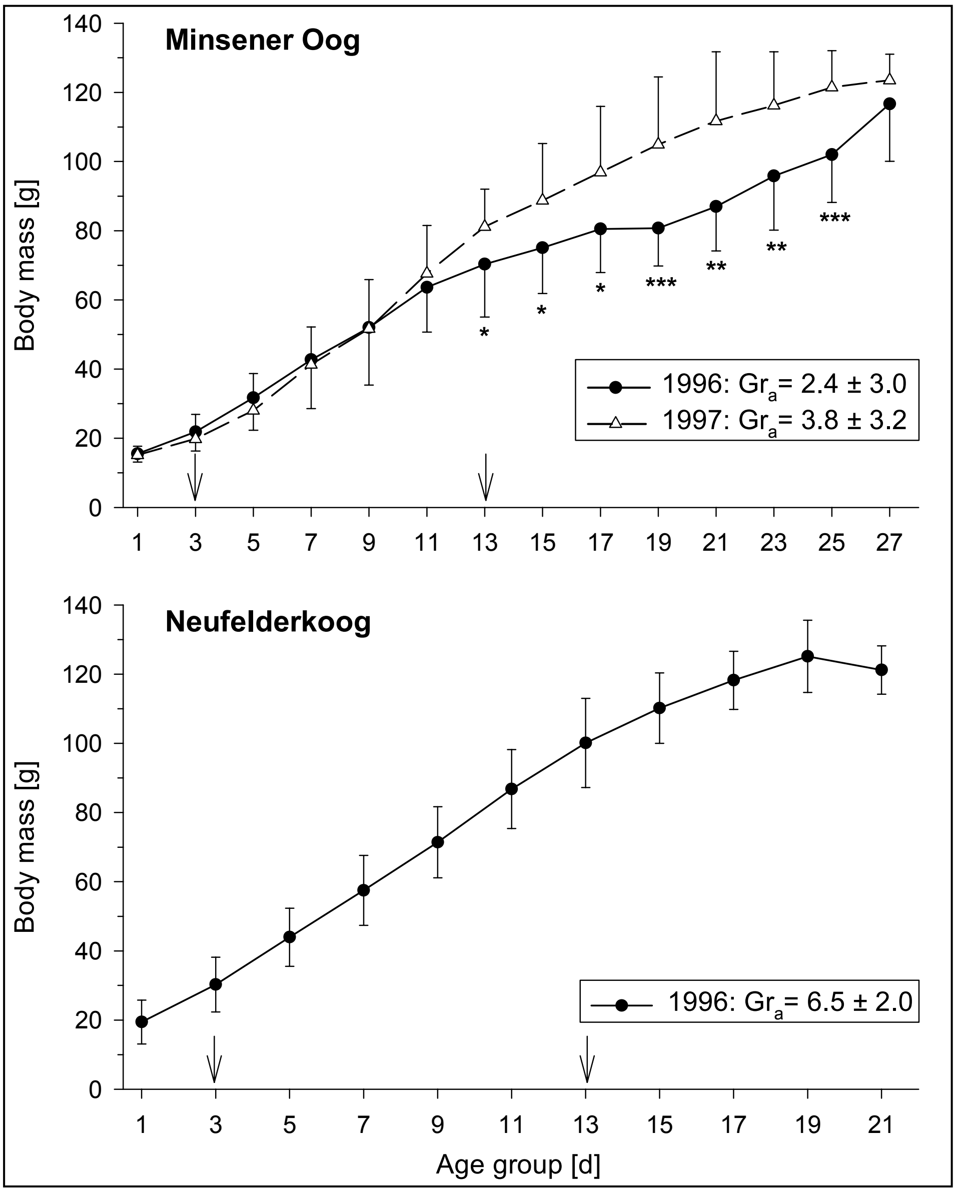

Fig. 5.12: Body mass development of Common Tern chicks at different colony sites in 1996 and 1997. For legend see Fig. 5.10. Age groups with n < 5 chicks are excluded from presentation. Because of a lack of data, growth curves of chicks of the Jadebusen are not presented. Significance levels according to U-tests. Note the different scalings of x-axes.

5.5. Discussion

5.5.1. Variations in hatching and breeding success and their causes

As revealed during the pilot study, hatching and breeding success mainly depended on factors like predation and flooding. Besides these components, hatching success of Oystercatchers was determined by sheep and cattle grazing at particular foreland sites on the mainland. Fledging success was restricted by further factors which affected chick vitality for no apparent reason. However, frequencies of lost eggs and chicks varied dependent on species or ‘species group’, breeding site, and breeding season. In the following paragraphs, these variations and their complex causes are discussed.

Hatching success

Predation

The most important factor which influenced hatching success in many cases was predation followed by flooding at several breeding places and colony sites of Oystercatchers and Avocets.

Except for Black-headed Gulls on Langeoog, hatching success was mostly higher at breeding sites on islands than at mainland sites because of lower predation. Large egg losses were observed at those places where ground predators occurred. Especially at Neßmersiel, the eastern Jadebusen, Westerhever, and Beltringharder Koog, foxes were presumably responsible for total egg losses (see 5.4.1.). Except for particular cases of total failures, the larids achieved higher hatching success in general than waders. Hatching success of Avocets altogether was higher than that of Oystercatchers, for example at Hedwigenkoog in 1996. At nearly all breeding sites, predation was lower in 1997 than in 1996, but only at few places, this result was supported by a definitely observed decrease in predator abundance. For example at the eastern Jadebusen and at Westerhever, no foxes were observed during the incubation period in 1997, in contrast to 1996. Corresponding to the decrease in frequencies of predated eggs, all species achieved higher hatching success in 1997 than in 1996 at most breeding sites, except for the Herring Gull.

The result that predation and hatching success varied between sites was presumably caused by varying abundances of predators. But, moreover, antipredator behaviour and habitat selection of the birds could have been of importance, too. In comparison to territorial birds breeding solitarily, colonial birds are regarded as to be more capable of defending offspring because of an effective antipredator behaviour (Beintema & Müskens 1987, Becker 1995). In general, this hypothesis is confirmed by the present results. But, a joint antipredator behaviour naturally is only effective if it is performed against predator species which are sensitive towards such attacks. Avian predators like Oystercatchers, gulls, and crows are mostly ‘sensitive species’ but nocturnal ground predators like foxes and martens are not. Therefore, colonial breeding can have a detrimental effect in habitats where mammalian predators occur (Southern *et al.* 1985, Becker & Anlauf 1988a). As an example of such a phenomenon, the Black-headed Gulls breeding on Langeoog in 1996 and 1997 could be mentioned. In contrast to the Oystercatchers breeding at the same place, these gulls suffered total egg losses in both study years. Nevertheless, breeding on islands should in principle be advantageous because pressure by ground predators is usually lower on the German North Sea islands than on the mainland coast (Melter *et al.* 1997). Except for the Black-headed Gulls mentioned above, this fact is reflected by the present results. The relatively low predation pressure is assumed to be one reason for the fact that larids prefer breeding on islands. In case of the Oystercatcher, the preferred selection of island habitats as well as the relative high hatching success observed are presumably caused by aspects concerning their feeding strategy (see below; Stock *et al.* 1987). In contrast, the feeding strategy of the Avocet, i.e. foraging on mud flats adjacent to the mainland coast, prevents settling on islands and thus selecting habitats with potentially and relatively low pressure by mammalian predators.

Besides the variations in hatching success dependent on species and breeding sites discussed above, interyear variations of predation and hatching success were found, especially in Black-headed Gulls, Oystercatchers, and Avocets. Obviously, the higher hatching success of these species in 1997 was caused by a decrease in egg predation which is partly explainable by a decrease in the abundance of predators at some breeding sites (see above). On the other hand, the observation that decreases in frequencies of predated eggs occurred in several species and at several breeding sites suggests that there were further mechanisms which reduced predation. One possibility is that potential predators could have fed on alternative prey in 1997 caused, for example, by a higher abundance of voles (e.g. Beintema & Müskens 1987). Another possible mechanism could have been a more effective exclusion of predation by the birds themselves in 1997 than in 1996. After they suffered frequent egg losses in 1996, the Avocets at Beltringharder Koog, for example, resettled on islands in shallow ponds in 1997. Furthermore, an influence of the Wadden Sea food supply on the decrease in predation and thus on hatching success as well as on breeding success of the birds is possible (for discussion see 5.5.1.). For example, Ens *et al.* (1992) and Brouwer & Spaans (1994) proved a positive influence of an auspicious food availability on hatching success which is possibly effected by an advantageous time allocation that allows for a more intensive parental care (e.g. antipredator behaviour).

Flooding and trampling

In Oystercatchers and Avocets, more or less frequent losses caused by flooding mainly occurred at the lower areas on the mainland of Schleswig-Holstein. In contrast to the annually varying frequencies of egg losses caused by predation, the losses caused by flooding were relatively constant between years. These losses are due to the preferred habitat selection of these birds. Because of their specific nesting and feeding behaviour, both species prefer settling on places close to the tidal flats influenced by high water tables and flooding (Gloe 1971, Nogueira *et al.* 1996, Ens *et al.* 1992, Becker & Anlauf 1988b).

Indeed, Oystercatchers mainly settle next to the level of mean high tide but they are present uniformly distributed in the remaining foreland as well. In sheep or cattle grazed habitats, more or less large egg losses caused by trampling occur regularly (Beintema 1982, 1986a, Witt 1986, Hötker & Kölsch 1993, Hälterlein 1996). During the investigations, large egg losses were found on those areas where cattle grazed the foreland to its outer edge (e.g. Neßmersiel in 1996). By the restriction of grazing on areas near the dike, these losses are evidently minimized but not absolutely prevented in any one of the observed forelands (see 5.2. and Fig. 5.3).

Thus, hatching and breeding success of Oystercatchers is obviously influenced by the distribution of the birds as well as the extension of agricultural land use in the foreland. Conclusions regarding causal connections between grazing and hatching success can only be drawn for breeding sites which are extensively grazed and extensively abandoned to its outer edge, respectively, as, for example, at Neßmersiel (see below). At Norderheverkoog, hatching success of Oystercatchers could have been lower on uncultivated areas than on pastures in 1996 because nesting sites adjacent to the level of mean high tide were flooded more spaciously and because abundance of breeding pairs in proportion was higher on uncultivated areas near the tidal flats than on grazed areas near the dike. In contrast, effects of grazing on hatching success could be studied better with the study area at Neßmersiel in 1996 (see above). At this site, extensive cattle grazing (0.5 cattle/ha) caused a reduction of hatching success of about 10 %. Oystercatchers breeding on intensively grazed pastures did not achieve any hatching success.

Further factors restricting hatching success

Abandonment of clutches and infertility of eggs and the death of embryos, respectively, were further phenomena restricting hatching success. In all species, corresponding losses were much less important than those elucidated above. Losses caused by non-hatched chicks were hardly observed except for the Herring Gull and except for few breeding sites of the other species monitored. In the case of Herring Gulls, the portions of chicks not hatched were relatively constant between sites and years. They were comparable to those found by other authors (see compilation in Kilpi 1990, Wilkens & Exo 1998). In contrast, considerable portions of non-hatched chicks observed in Black-headed Gulls, Avocets, and Oystercatchers occurred only in particular cases. Disturbances of breeding birds by flooding, predators, or sheep and cattle are able to induce abandonment of clutches and, consequently, the death of embryos. Indeed, in the three species mentioned, those losses often were related to the occurrence of flooding events (e.g. at the eastern Jadebusen and Schobüller Bucht) and of predators (e.g. on Langeoog in 1996). At Dieksanderkoog (1997), disturbances by sheep in an officially non-grazed area could be responsible for abandonment of clutches in Avocets (see Schulz 1987).

‘Unusually high proportions’ of non-hatched chicks not explainable by direct influences or species-specific conditions were not observed during the study. Thus, influences of environmental pollution caused by pesticides and industrial chemicals presumably can be neglected (Becker *et al.* 1998).

Breeding success

During the study, breeding success as well as hatching success varied between the different bird species, study areas, and study years. In comparison to other species, Herring Gulls achieved relatively high and constant reproductive and breeding success. The corresponding values achieved by Black-headed Gulls, Common Terns, and Avocets altogether were lower and they were subject to higher intersite and interyear variations.

Predation and flooding

In contrast to hatching success, predation seems to be quite unimportant as a factor limiting fledging success of Avocets (Hötker & Segebade 2000). According to long-term observations at breeding sites in Schleswig-Holstein, foxes assumed to be unable to predate Avocet chicks, and avian predators seemed to be of only marginal significance as chick predators. In case of the latter, no correlation between population sizes and breeding success of Avocets was found during the investigations of several years. On the contrary, an association between weather and breeding success of Avocets existed. Especially cold and windy weather, which is often connected with storm tides, seemed to influence chick survival probabilities. The very low breeding success in 1996 was partially caused by events described above.

On the other hand, the Black-headed Gull and Common Tern chicks as well as their eggs were exposed to influences like predation and flooding. However, these influences varied in different ways. Except for the habitat selection of the parental birds, these fluctuations can be explained by the advancing of physical development, the changing of defensive readiness during the breeding season, and possible seasonal fluctuations in abundance and preference of predators (Sordahl 1982, Becker 1984, Sudmann *et al.* 1994, Becker 1995). Moreover, the predation pressure could be stronger during the rearing period than during the incubation period because of some additional potential predator species (e.g. Sudmann *et al.* 1994).

During the study, the proportional numbers of predated nestlings of Black-headed Gulls and Common Terns were larger in nearly every case than the proportions of predated eggs. In case of the Herring Gull, a comparable trend could not be proved. There is a further example for an increasing hardiness of the offspring against direct external influences during the breeding season: The Common Terns breeding at the Jadebusen in 1997 suffered a total breeding failure induced by flooding, although they achieved a sufficient hatching success. In contrast, the Black-headed Gulls breeding at the same site achieved a breeding success (Becker & Anlauf 1988b). The chicks of the latter hatched earlier and survived the high tide possibly by swimming (Behnke pers. comm.).

State of nutrition within the ecosystem

As shown in the previous paragraphs, extent and occurrence of egg and chick losses caused by predation and flooding were more or less regionally limited. In addition to these, influences taking place for no apparent reason also affected chick survival (‘chicks found dead’). In the following paragraphs, these causes are expected to be revealed by linking the various parameters studied during the monitoring project. It will be demonstrated that the results of monitoring breeding success are able to define particular environmental influences. On the basis of such results, detailed studies could be conducted in the future to quantify deficiencies in the birds´ environment (5.5.3.).

Possible causes for a suboptimal chick development are malnutrition, hypothermia, and disease. According to intensity, duration of exposition, and stage of chick rearing, these factors are able to effect growth retardation or even death, and thus, to cause a decrease in breeding success (e.g. Beintema & Visser 1989a, Mlody & Becker 1991, Drent *et al.* 1992, Klaasen et al 1994, Kersten & Brenninkmeijer 1995).

Appropriate feeding conditions naturally depend on quality and availability of feeding objects. The latter aspect is, first of all, determined by frequency, density, and distribution of prey but also by the species-specific feeding ecology of the birds. On the other hand, the feeding strategies are influenced by factors like weather, tide, competition for food, etc. (Dunn 1975, Safina *et al.* 1988, Hario 1990, Massias & Becker 1990, Becker & Specht 1991, Ens *et al.* 1992, van Klinken 1992, Nordhuis & Spaans 1992, Becker *et al.* 1997b).

Besides benthic organisms and fish, Herring Gulls of the North Sea coast supplementary feed on fishing scraps and human garbage. Black-headed Gulls feed less opportunistically. During the breeding season, they occur less frequently as birds scavenging on discards from fishing vessels and as visitors of human dumps than Herring Gulls. Though, Black-headed

Gulls breeding on the mainland use agricultural fields as foraging habitats (Spaans 1971, Glutz von Blotzheim & Bauer 1999a, Gorke 1990, Becker 1993c, Hüppop 1993). On the contrary, the mainly fish-eating Common Terns, and furthermore Oystercatchers and especially Avocets, which both feed on benthic organisms, are specialists concerning their feeding strategy (Glutz von Blotzheim *et al.* 1986, 1982, 1999, Becker *et al.* 1987).

The results of the two-year monitoring give hints on varying food supplies between breeding sites and, as the most important aspect, between years. Especially the results found in Common Terns prove a high variability in food supplies between different colony sites. In 1996 and 1997, more dead chicks were found on Minsener Oog than in colonies on the mainland. Moreover, in 1996 the chicks of Minsener Oog significantly grew with a lower average rate than those of Neufelderkoog, where, in addition, breeding success was higher. In conclusion, it can be assumed that chicks starved to death more frequently on the island Minsener Oog than at the mainland site of Neufelderkoog because the availability of marine food depends considerably on the tide. On the contrary, at sites on the mainland coast, there are potentially additional limnetic food sources (Frank 1992, Becker *et al.* 1997c). Similarly, the Herring Gulls are able to use alternative food sources if there are regional or temporal food shortages within the ecosystem. As mentioned above, such alternatives, for example, are dumps on the mainland (Wilkens & Exo 1998). Black-headed Gulls, Oystercatchers, and Avocets do not use comparable alternatives. Interestingly enough, just these species had lower hatching success in 1996 at all breeding sites which were observed over the two years. In addition, in Black-headed Gulls and Avocets higher reproductive success and lower chick mortalities, respectively, were found. The ascertained body mass development, growth rates, and age-dependent variations in chick mortality of Black-headed Gull clearly point out a more favourable nutritive state in 1997, in comparison to 1996. In 1997, the chicks grew with a higher rate than in 1996 and those of different rearing stages were mostly heavier than chicks of comparable age groups the year before. Furthermore, not only chicks hatched at third position of the hatching sequence, but also ‘first’ and ‘second chicks’ died, especially in the first days of life at Westerhever in 1996, possibly because of a relative strong sibling competition. A comparable observation is missing for the colony at the Jadebusen because brood sizes were reduced artificially by removing eggs from some clutches for another monitoring project. On the other hand, the mortalities of a few-day old nestlings were considerably lower and only the youngest, less vigorous siblings were affected in 1997 (Langham 1972).

What could have been the reason for the assumed unfavourable nutritive state of the year 1996? The differences in breeding success (in the case of Black-headed Gulls connected with a reduced chick development) were only found in species which feed on benthos organisms for the most part. Accordingly, it can be assumed that just this food source was restricted in 1996. A main cause for this deficiency could have been the long lasting ‘ice winter’ 1995/1996 which was characterized by eastern winds and a long period of extreme frost. Consequently, significant lower densities of benthic organisms were ascertained in comparison to the years before until spatfall started towards the end of July in 1996 (Dittmann pers. comm., see also Herlyn 1996, Oeschger 1997). In addition, the ‘state of young fish' in the North Sea was more favourable in 1997 than in 1996 (Dornheim & Wegner 1996, 1997). Maybe, this fact had an intensifying effect on the breeding failures of the Black-headed Gulls. In the more suitable indicator species for this prey, i.e. the Common Tern, differences in breeding success on Minsener Oog did not occur during the two years of study but, indeed, significant differences in growth patterns of the more than two-week old and more pretentious chicks were observed.

Weather

Besides the influences of the nutritive state, the present results indicate that the breeding seasons probably were influenced by weather conditions as well. Common Terns mainly prey on marine and limnetic fish by locating them optically. Therefore, rain and wind hinder the foraging of terns by inducing behavioural changes of prey fishes (vertical migrations) and by perturbing the water surface (Dunn 1975, Taylor 1983). This leads to a deterioration in the feeding conditions of Common Terns. Especially rain also reduces growth and vitality of still heterothermic chicks by affecting the time budgets of feeding and brooding parents. Consequently, rain leads possibly to malnutrition and hypothermia of the chicks (Becker & Finck 1985, Beintema & Visser 1989a, b, Hötker 1994, Hötker & Segebade 2000). Thus, 'bad weather' affects the development of tern chicks in a direct as well as in indirect way. Chicks of the other species of the monitoring program primarily are affected by direct influences which have negative effects on vitality, especially during early rearing stages.

In contrast to the Black-headed Gull chicks, the young of the Common Tern on Minsener Oog hardly grew with a higher rate in 1997 than in 1996. Only just from an age of about two weeks, a significant growth retardation and a higher mortality of chicks of an advanced age occurred in 1996 in comparison to 1997. This observation could potentially be related to the already mentioned deficiency of young fish in the North Sea. Accordingly, a comparable development did not happen in chicks at Neufelderkoog because of reasons discussed above. However, if only the scarce food supply in 1996 was responsible for this development, more chicks would already have died at an early stage of the rearing period in 1996, and the average daily increase in body mass during the stage of linear growth would have been smaller. But this was only partly true. It is probable that the weather had an additive effect on the retarded development of the chicks. The assumed influence of the weather is emphasized by the fact that increased chick mortality also was found in the case of Black-headed and Herring Gull towards the end of June (see 5.4.3.). Differentiated data concerning the phenology of chick mortality in Avocets are not available. However, according to observations made in Schleswig-Holstein, a high Avocet chick mortality caused by weather conditions in June of 1996 can be assumed, too (Hötker & Segebade 2000).

In this study, suitable weather data, which permit comparative statistical calculations, were not available. The future inclusion of such data in analyses is recommended. Though, the records of some fieldworkers indicate that the weather in the middle and at the end of the June of both years was partly characterized by strong winds and cold showers. Maybe these facts could explain the maxima of chick mortalities of most species and at most sites during the corresponding periods of rain. Only in Herring Gulls breeding on Mellum and in Black-headed Gulls breeding at Westerhever in 1996, such maxima of mortality were not found.

Maybe the observation mentioned first was caused by the early beginning of hatching, the latter could be explained by the decimation of the number of nestlings by predators.

Table 5.4: Examples for hatching and breeding success of former studies compared to those of this study. Mentioned are mean values or ranges found during one or several study years. Hatching success in % of all eggs found, breeding success in fledglings per pair and clutch, respectively. S-H= Schleswig-Holstein, *= see Fig. 5.13.

Region	Year	Hatching success	Breeding success	Authors
Herring Gull				
Langeoog	1996/1997	82-86	0.8-0.9	this study
Mellum	1996/1997	87-98	1.2-1.5	this study
Mellum	1979-1981, 1990	67-84	0.9-1.3	Becker & Exo 1991
Mellum	1995	77	1.3	Wilkens & Exo 1998
Black-headed Gull				
Langeoog	1996/1997	0	0	this study
Westerhever	1996/1997	65-87	0.1-1.6	this study
Lower Elbe	1971-1974		0.3-0.6	Goos in Zang *et al.* 1991
Common Tern				
Eastern Jadebusen	1996/1997	0-55	0	this study
Minsener Oog	1996/1997	89-94	0.6-0.7	this study
Augustgroden	1980-1985	46-85	0.0-1.5	Becker & Anlauf 1988a,b
Baltrum	1993-1995	83-92	0.3-1.8	Becker *et al.* 1997
Minsener Oog *	1981-1995	75-99	0-1.5	Becker 1992, Becker *et al.* 1997a, supplemented
Jade	1981-1996	87	0.8	Becker 1998
Oystercatcher				
Langeoog	1996/1997	48-97		this study
Norderheverkoog	1996/1997	1-15		this study
Mellum	1986-1988	28-50		Pleines in Zang *et al.* 1995
Nordender Groden	1994	25		Thyen 1996a
Forelands of S-H *	1992-1995	0-76		Hälterlein unpubl.
Sönke-Nissen-Koog	1989	36-100		Andresen 1989
Langeneß	1986	61		Becker 1987
Avocet				
Eastern Jadebusen	1997	45		this study
Beltringharder Koog	1996/1997	27-59	0.02-0.2	this study
Nordender Groden	1994	9		Thyen 1996a
Beltringharder Koog *	1988-1995	14-73	0.1-1.5	Hötker & Kölsch 1993, supplemented
Fahretofter Westerkoog	1994/1995		0.3-0.5	Hötker unpubl.

5.5.2. Assessment of hatching and breeding success

In the following paragraph, the current results will be assessed although some important requirements for a purposeful assessment are still needed (see below, 5.5.3.). Hence, the following evaluation is merely a provisional one.

To assess the ecological state of the Wadden Sea ecosystem with the aid of breeding success and to estimate if breeding success is a natural one, comparative values determined by long-term studies are required. However, such a data basis does not exist for the total area of the Wadden Sea yet. Therefore, a provisional comparison is made by means of values which were ascertained during former studies, although their temporal and spatial validity may be restricted (Table 5.4; Fig. 5.13).

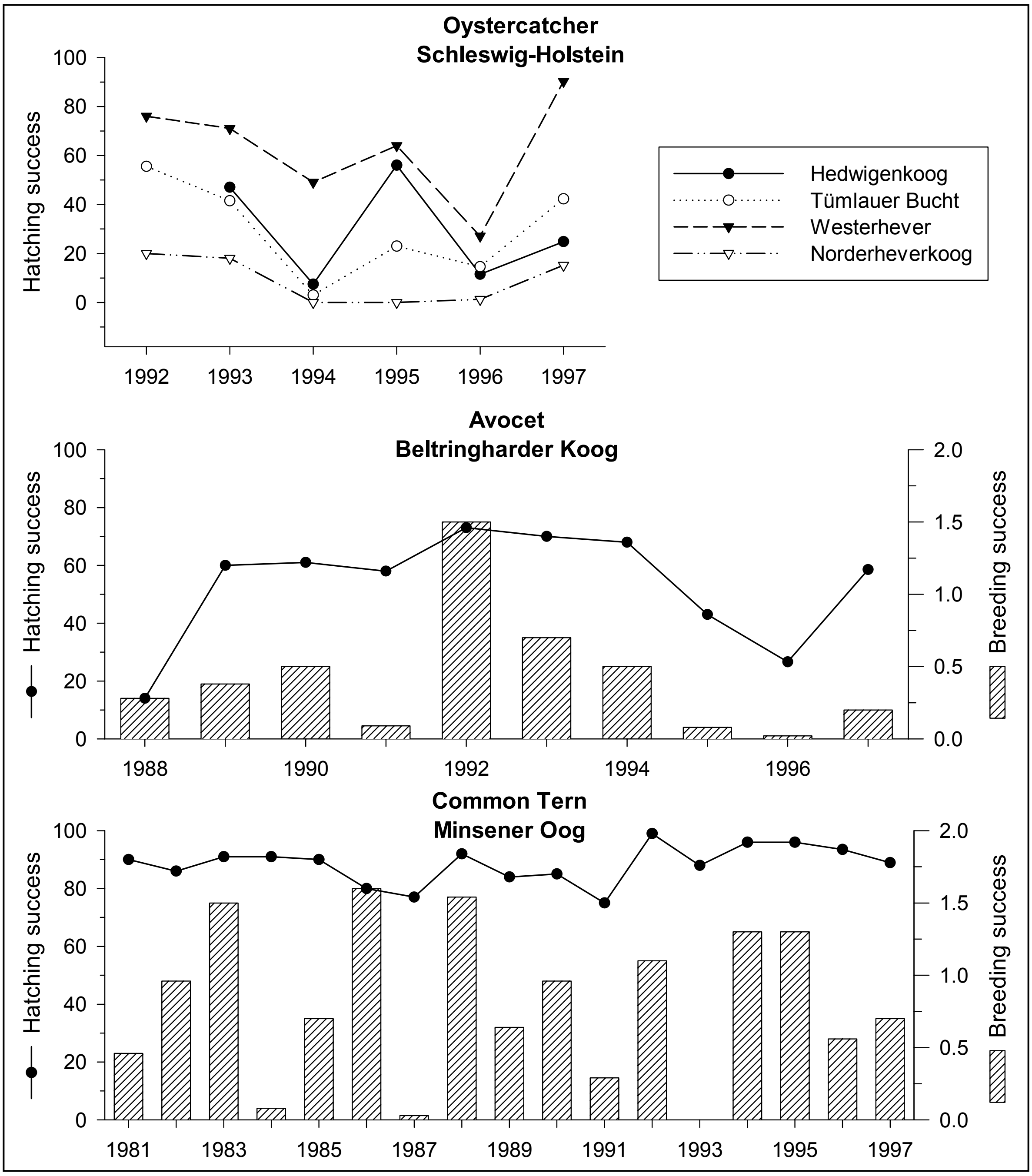

Fig. 5.13: Examples for hatching and breeding success of different species, breeding sites, and seasons. The figure is based on data from B. Hälterlein (Oystercatcher), H. Hötker (Avocet) and P.H. Becker (Common Tern; see also Table 5.4). Hatching success in % of all eggs, breeding success in number of fledged chicks/clutch.

An assessment of the monitoring results with regard to coastal bird conservation, is carried out by comparing topical breeding success with empirical values of minimum reproductive output that is needed to keep the current population size of a species (see 5.5.3.). Because of the short period of study, the data collected during the pilot studies are not suited to draw conclusions regarding future changes in breeding bird stocks. To draw such conclusions, a long-term monitoring of breeding success is required.

Except for total failures of altogether seven Black-headed Gull, Common Tern, and Avocet colonies in both study years, the results of hatching and breeding success were on a low to average level in 1996. In 1997, the values were even on an average to a high level, in comparison to results of former studies (Table 5.4; Fig. 5.13). In 1997, hatching success of Oystercatchers breeding on Langeoog and at Westerhever was evidently extremely high.

In view of population dynamics, only Herring Gulls achieved sufficient breeding success at all sites and in all years in comparison to the other monitored species. The minimum breeding success to keep the current Herring Gull population size is 0.6 chicks/breeding pair (Glutz von Blotzheim & Bauer 1999a). Thus, reproductive outputs achieved by Herring Gulls in 1996 and 1997 were mostly higher than the minimum output. In Black-headed Gulls, comparable results should have been obtained, at best, at the eastern Jadebusen and at Westerhever in 1997. In case of Common Terns, at least 0.8 to 1 chicks/breeding pair are needed to maintain population size (Becker 1998, DiConstanzo 1980). These values were only exceeded by the terns breeding at Neufelderkoog in 1996. No sufficient success was found in case of all examined Avocet colonies (minimum reproductive output: 1.2-1.6 chicks/pair; Glutz von Blotzheim *et al.* 1986). According to the observed hatching success, the Oystercatcher should have bred sufficiently successful to achieve the minimum breeding success, at best, on Langeoog (in 1996 and 1997), at Neßmersiel (1996), and at Westerhever (1997).

How can these results be assessed regarding the causes for variations in breeding and hatching success discussed in paragraph 5.5.1., and in which way can they be used as indicators for the ecological state of the Wadden Sea ?

'Catastrophic' failures during the study were only caused by flooding and predation. Thus, large breeding losses were attributed to local or regional, but certainly not to ecosystem-wide 'problems'. Though, the possible significance of the actual food availability for predators (see 5.5.1.) and the prospective significance of an expected sea level rise has to be considered in this context (e.g. Becker & Anlauf 1988b, Hofstede 1994). The supposed food shortage for some species, which feed on benthic organisms, could have been of significance for the total Wadden Sea. Such shortages cannot be quantified by monitoring breeding success but require more detailed studies. However, the results suggest that the assumed shortage of benthic and possibly also pelagic food in 1996 not only was a relative one in comparison to 1997 but an absolute one: If the reproductive output of the birds exceeded minimum breeding success during the two studied seasons, then it most certainly did in 1997.

5.5.3. Consequences of the study for a trilateral monitoring program

Position of monitoring breeding success within the TMAP

To guarantee an effective conservation of the ecosystem, the aim of the trilateral management is to achieve the full scale of habitat types which belong to a natural and dynamic Wadden Sea. Therefore, the following Ecotargets were adopted on a trilateral level: extending the natural, dynamic, and undisturbed areas of the offshore zone, beaches and dunes, tidal areas, salt marshes, and estuaries; adjusting the concentrations of naturally occurring substances (for example nutrients and heavy metals) within the ecosystem on a natural level; reducing the discharges of non-natural substances (for example pesticides) to zero. Because of the ecosystem-wide presence of the birds, supplementary Ecotargets were adopted. A favourable food availability, a natural breeding success, sufficiently large undisturbed roosting and moulting areas, and natural flight distances are supposed to be guaranteed (Bakker *et al.* 1997).

As 'ecological warning signals' can be recognized, counter-measures can be introduced, and inspections of success of counter-measures can be carried out only by accompanying research and supervising, the necessity of a monitoring program as a tool and a premise of a lasting environmental conservation is undisputed (Nettleship 1991). The pursuance of the Ecotargets to protect the Wadden Sea and the coastal birds requires a monitoring program, too. Because the Wadden Sea is extensive and diversely structured, such a program has to be conducted with differentiated parameters. Therefore, the TMAP is based on several 'Issues of Concern' with a large number of monitoring parameters to examine (see introduction; CWSS 1995). Thus, coastal birds get importance on two different levels within the trilateral Wadden Sea conservation. On the one hand, they themselves are objects of defined conservation efforts. On the other hand, just these organisms can be used as instruments to accomplish the aims of the Wadden Sea conservation by using the great indicator value of their biology in different monitoring projects of the TMAP (monitoring migratory birds, monitoring population sizes of breeding birds, monitoring chemicals in seabirds, monitoring breeding success).

As elucidated above, natural breeding success is an explicit aim of the trilateral Wadden Sea conservation. To guarantee natural breeding success, this parameter has to be determined and monitored continuously. Already this fact is an important argument for the necessity of monitoring breeding success as part of the TMAP.

But there are further reasons why monitoring breeding success should be established. These reasons base on principles of coastal birds' population biology. Besides the parameters 'immigration' and 'emigration', size and maintenance of breeding bird populations is determined by additional parameters. One of the most important is the annual breeding success of a population. Together with the parameter of mortality of juvenile individuals, it determines the future number of sexually mature birds which become part of the breeding bird population and thus contribute to the continued existence of the population. To maintain a current population size, the leaving of birds caused by death or emigration must be made up of sexually mature young produced in the own population or by immigration of birds from other populations. In coastal birds, the turnover of breeding individuals within the population passes very slowly because most coastal birds are 'K strategists'. These birds are long-lived, their juvenile development takes a relatively long time, they reach sexual maturity relatively late, and their annual reproductivity is low (e.g. Bezzel & Prinzinger 1990, Dunnet *et al.* 1990).

From these conditions, important consequences for the Wadden Sea and coastal bird conservation and for the position of monitoring breeding success within the TMAP emerge. As for species conservation in general, monitoring population size has an essential significance for the conservation of coastal birds. However, only those environmental influences are recognized by monitoring population size which affect the current stocks of breeding birds in a direct way. Gradual environmental changes influencing breeding success (for example discharges of harmful chemicals, latent food shortage, etc.) frequently have lasting effects on bird population sizes. By conducting censuses of breeding birds exclusively, those gradual influences should only be detected with a considerable delay because of population dynamics of coastal birds elucidated above. In case of the example for a development of a population presented in Fig. 5.14, a decrease in population size of about 10 % occurs six years after breeding success decreased from 0.6 to 0.5 fledglings/pair. Because of an assumed counting error of 10 %, this reduction in breeding bird numbers as well as its cause, presumably would not be recognized even after this period.

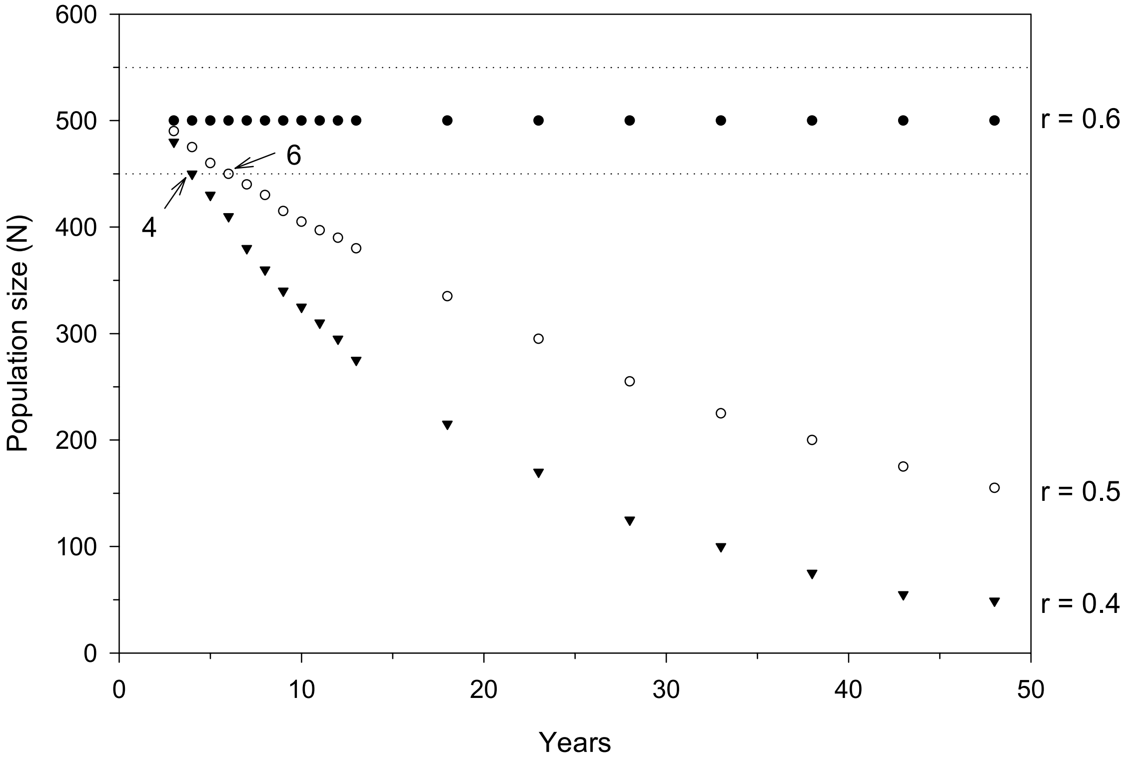

Fig. 5.14: Theoretical development of a population during 50 years. Assumed are variable breeding success (in number of fledglings/pair) and a mortality of 50 % in the first year of birds' life and 15 % in birds older than one year. Furthermore, a initial population of 500 breeding pairs and sexual maturity from an age of 3 years are assumed. The dotted lines represent a presumed counting error of 10 %, the arrows label the points in time when population size decreases by 10 %.

As the following explanation substantiates, it is sometimes even impossible to detect environmental changes which affect breeding success of a population by an exclusive monitoring of population size. At single colony sites, a current population size can be maintained, although breeding success stayed below minimum breeding success for years. This phenomenon can be explained by immigration of pairs from ‘reproductive sources‘ to ‘population sinks’, for example, single colonies (Pulliam 1988, Exo *et al.* 1996). Thus, a current stock of breeding birds can possibly be maintained on a particular level, although environmental influences occur which cause disturbances in the breeding biology of the birds.

Because of these ecological circumstances, an early recognition of environmental changes which influences stocks of breeding coastal birds, an early introduction of counter-measures and thus, an effective conservation of the Wadden Sea ecosystem and the coastal birds inevitably requires the monitoring of breeding success besides monitoring population size (Becker 1992, Exo *et al.* 1996).

The programs of monitoring population size and monitoring breeding success are important components of the TMAP. They are both needed to recognize and to supervise occurrence and effects of environmental changes within the ecosystem. As the present results of the pilot studies prove, particular environmental changes can be specified and even localized by monitoring breeding success and by observing body mass development of chicks, respectively. In the future, such results can be used as indicators for the need of detailed studies to quantify environmental deficiencies determined by monitoring breeding success. Besides the factors discussed in 5.5.1., the pollution of the ecosystem by harmful chemicals is a further significant element which influences breeding success and body mass development of chicks (e.g. Becker 1992, Becker *et al.* 1992, Burger & Gochfeld 1988, Gochfeld & Burger 1988). Although the effects of such a ‘disturbance’ can partly be detected by studying hatching success in the framework of monitoring breeding success, the causes, the nature, and the extent of pollution can only be defined and quantified by monitoring chemicals in seabirds. Therefore, monitoring chemicals in seabirds is a further essential part of an ‘early warning system’ (see above).

An effective Wadden Sea conservation and, especially, an effective conservation of the avifauna of the ecosystem can only be achieved by establishing each of the three programs described in the above discussion within the TMAP. By combining these programs, all ‘Issues of Concern’ of the trilateral monitoring program (see 1.) can be supervised. Already the results of the two-year pilot study yield conclusions concerning the influences of agricultural use of salt marshes, of climate, and, partly, even of fisheries on Wadden Sea habitats and their life communities. Besides these issues, the remaining ‘Issues of Concern’, i.e. pollution and recreation, can be studied and monitored by a combined application of monitoring breeding success, population size, and chemicals in the future.

Demands on monitoring breeding success

As valuable as monitoring of breeding success is, as pretentious is its implementation in view of the temporal scope and the selection of suitable study areas and indicator species. It must be the aim of the program to ascertain region- and species-specific mean values of hatching and breeding success and of parameters of chick development by continuous long-term studies. Reasons for this high demand are provided by the results of the two-year pilot study, which conspicuously varied between sites, species, and years.

Target species

As recommended in the methodological guideline, such species should be selected as monitoring objects which, on the one hand, have distinguished breeding and feeding strategies and, on the other hand, are representative for the Wadden Sea or for characteristic parts of it. A suitable spectrum of monitoring species is characterized by species which, if possible, represent all ecological life-forms found in the Wadden Sea. In view of the Wadden Sea conservation, this requirement means that each habitat can continuously be assessed concerning its aptitude as foraging and breeding habitat. Negative ecological changes in the ecosystem only can be detected and even localized if as much distinguished life-forms as possible are monitored. The study documented in this report is an example for the necessity of monitoring different breeding bird species. If, for example, only the Herring Gull was exclusively observed, the results would have led to misleading conclusions.

The spectrum of species monitored in the pilot study represented the major part of the occurring ecological life-forms, but it was incomplete. A further important life-form could be studied by the future inclusion of the Lesser Black-backed Gull (*Larus fuscus*) in the monitoring program. With regard to the number of breeding pairs, this gull species has been gaining in importance for about 25 years (Exo 1994, Heckenroth & Laske 1997). According to several investigations, the specific foraging strategy and the adaptability of this species could be responsible for the increase in breeding pair numbers. In comparison to the Herring Gull, Lesser Black-backed Gulls seem to be able to use fishing discards in a more effective way, especially in offshore regions (Nordhuis & Spaans 1992; Hüppop *et al.* 1994). By monitoring breeding success of the Lesser Black-backed Gull in addition to the present monitoring species, influences of fishing as one of the ‘Issues of Concern’ of the TMAP could be studied more accurately than during the pilot study. Therefore, an increase of the spectrum of monitoring species is hereby expressly recommended.

Study sites and extent of the project area

Dependent on specific preferences, coastal birds settle all occurring terrestrial habitats of the Wadden Sea ecosystem. The breeding places are considerably distinguished by their inventory of available food, of predator species (abundance and occurrence), and of structures concerning the topography and vegetation. Thus, the ecological quality regarding reproduction of the birds varies between breeding places. As the current results prove, these varying conditions cause varying hatching success, breeding success, and body mass development of chicks. Therefore, natural breeding success as one of the Ecotargets of the Wadden Sea conservation (see 5.5.3.) cannot be stated with an ecosystem-wide validity. Rather, natural breeding success depends on the quality of a breeding place. To determine natural breeding success and to guarantee it by suitable conservation measures, success must be monitored on as large a number of study sites as possible.

Caused by the high variability of breeding success between sites, there is a risk that the ecological state of the Wadden Sea and the future development of breeding bird numbers is assessed incorrectly. If, for example, only optimal breeding and colony sites with naturally high levels of breeding success would be monitored, the monitoring results could be misinterpreted as indicators for stable breeding bird populations and a healthy ecosystem. Without the knowledge of breeding success achieved at different, i.e. optimal, suboptimal or even pessimal sites, the ‘early warning system’ (see above) would not work.

To use the tool of monitoring breeding success expediently, the knowledge of quality and quantity of the variations in hatching and breeding success between breeding sites is needed. This knowledge can only be gained by studying either a large number of sites or a representative range of study areas distributed over the whole Wadden Sea area. As suggested in the methodological guidelines of Exo *et al.* (1994, 1996), larids and Avocets should be studied on at least two sites per state bordering on the Wadden Sea (Denmark, Schleswig-Holstein, Lower Saxony, the Netherlands). Hatching success of Oystercatchers should be studied at four places per state.

During the pilot studies conducted in Schleswig-Holstein and Lower Saxony, the elucidated requirements on the selection of suitable study areas were met to a large extent. However, the future continuation of monitoring breeding success urgently requires an extension of the project area to Denmark and the Netherlands. The conditions of Danish and Dutch breeding places and colony sites are partly different from German ones. As, for example, Becker *et al.* (1997a) presume, foraging habitats of Common Terns breeding on the Dutch island Griend could be less valuable than those located in the German Wadden Sea area. Melter *et al.* (1997) report that predator abundances are mostly higher on Danish North Sea islands than on German ones. These examples indicate that the habitats located in the German Wadden Sea area do not represent the whole range of qualitatively distinguished habitats occurring in the ecosystem. Therefore, monitoring breeding success only then yields results of ecosystem-wide significance when the project area is extended to Denmark and the Netherlands. The extension of the project area as well as the selection of the recommended number of study sites is demanded vigorously.

Temporal scope and continuity of the program

Besides studying suitable and meaningful monitoring parameters, regularity and continuity are the most important aspects of each monitoring project. That is absolutely valid for the trilateral monitoring program and, especially, for the monitoring of breeding success as part of the TMAP, too: A meaningful evaluation of the results and, thus, of the current ecological state of the Wadden Sea only is feasible if long-term trends and current deviations from this trend are known.

To provide natural resources and to guarantee natural breeding success as demanded by the trilaterally adopted Ecotargets, ‘the region- and species-specific naturalness’ of these parameters must be defined at first. The ‘natural state’ can only be defined by long-term mean values of several biological parameters. Thus, the requirement of carrying out the monitoring continuously is already caused by statistical reasons. Besides the ascertainment of long-term trends, the determination of deviations from these trends is a further aim of monitoring breeding success. By detecting such deviations, conclusions concerning the ecological state of the Wadden Sea and its avifauna are supposed to be drawn, and, if necessary, counter-measures are expected to be introduced in time. Just short-term environmental changes, i.e. ‘rare events’ according to Nisbet (1989), are expected to be recognized and influences of these events are supposed to be evaluated by means of the knowledge of long-term trends. By collecting data non-continuously, the significance of ‘rare events’ could be over- or underestimated. Consequently, that would have negative effects on a purposeful Wadden Sea and coastal bird conservation. Possibly, the values of hatching and breeding success ascertained in the framework of the pilot project in 1996 could be mentioned as examples for a negative effect of a ‘short-term environmental change’. An exclusive assessment of these results certainly would not have given an accurate description of the ecological state of the Wadden Sea.

Hence, the natural state of the Wadden Sea in the view of the birds as well as deviations from this state are supposed to be recognized and defined by means of monitoring breeding success. To guarantee this function of the monitoring project, it must inevitably be carried out without exception in every season and without any time limit. Therefore, the integration of monitoring breeding success into the TMAP as soon as possible and its continuous annual conduction is urgently demanded.

5.5.4. Assessment of the method

The aim of monitoring breeding success is to support the protection of coastal birds and the Wadden Sea ecosystem. To carry out the monitoring, a method is required which, on the one hand, yields exact and reproducible results and which, on the other hand, is not inconsistent with the conservation efforts (for example by disturbing the breeding performance of the birds). The methodological guideline (Exo *et al.* 1996) was developed according to these principles. As the results and the experiences obtained during the two-year studies indicate, the employed methods provides scientifically correct, repeatable, and meaningful results. Moreover, the method is very useful in view of nature conservation, too, if the monitoring is strictly carried out according to the methodological instructions.

In view of nature conservation, the field work is problematical in so far as the breeding place inspections could disturb the breeding of the birds directly or indirectly, for example by encouraging predation. As regards visible and quantifiable effects, these reservations proved to be unfounded. In course of the pilot studies, indications of disturbances of the breeding birds were hardly found. For example, egg losses caused by the abandonment of clutches were rarely recorded, and no hints of an increased predation of eggs or chicks caused by the studies were found. Because of experiences made in several former studies (see compilation in Exo *et al.* 1994; Becker 1998), negative effects of fencing-in colony areas and nesting sites were not expected in advance. Accordingly, hints of negative effects of the fences were not found during the studies.

Furthermore, no deficiencies concerning the practical applicability of the methodological guidelines were found during the two-year project. The recommended maximum duration of nest inspections was always obeyed. Thus, an excessive disturbance of the birds as well as the temporal scope of the examinations were kept within limits. Besides the temporal one, the expenditure regarding personnel was justifiable and feasible, too. In both study years, the continuous observation of a large number of study sites was always guaranteed.

Except for the Redshank, whose hatching success was not studied for reasons of nature conservation (see Introduction), the whole species spectrum recommended in the methodological concept as well as all recommended parameters of breeding success were studied successfully. In case of the Avocet, it emerged that some of the methodological instructions are too rigid. According to experiences gained at breeding sites in Schleswig-Holstein, even in ‘unsuited colonies’ breeding success can be ascertained with an adequate precision under particular conditions. At Dieksanderkoog, a large and non-isolated colony was studied in 1997. Migrations of Avocet families between colonies occurred only at a low extent at this site and, presumably, these migrations did not effect the precision of the ascertained value of breeding success. Furthermore, breeding success of Avocets can obviously be ascertained even without clutch censuses and without entering the colony if ‘suitable study sites’ are selected (Hötker and Grünkorn pers. comm.).

Besides the methodological additions discussed in 5.5.3., the future application of monitoring breeding success absolutely demands the observance of methodological minimum requirements. The recommended intervals of nest inspection (6 d) and the intervals of body mass measurement (3 d), respectively, as well as the demanded sample sizes are such methodological minimum requirements. Though, they are well suited compromises between the aspects of ‘reproducible and exact results’ and ‘nature conservation’.

Causes of clutch and chick losses, hatching and breeding success, and chick development are important and well suited parameters to describe the annual courses of breeding and, hence, to asses the ecological state of the Wadden Sea. However, the following conditions must be met to obtain meaningful and exact values. It is necessary to determine the fate of a clutch and the date of hatching, to assign larid chicks to defined nests, to record the body mass development of chicks, to determine the point in time of fledging, and to compare data collected in several species and years and at different regions. To meet these requirements, the inspection intervals have to be as short as possible and the sample sizes have to be as large as possible. On no account, sample sizes should be smaller and inspection intervals larger than demanded in the view of nature conservation. On the development of the methodological guidelines of monitoring breeding success, Exo *et al.* (1994, 1996) considered interests of nature conservation in a sufficient way. To guarantee an effective Wadden Sea and coastal bird conservation, the methodological instructions concerning the inspection intervals and the sample sizes should not be changed on any account.

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Lebenslauf

Name, Vorname: Thyen, Stefan
Geburtsort: Lastrup, Landkreis Cloppenburg
Geburtsdatum: 17. September 1965
Staatsangehörigkeit: deutsch

Schulausbildung

1972 – 1976	Grundschule Lindern
1976 – 1985	Orientierungsstufe und Gymnasium Löningen
1985	Allgemeine Hochschulreife

Berufsausbildung

1987 – 1989	Berufsfachschule –Landw.-techn. Assistent–, BBS III Lüneburg, Norddeutsche Pflanzenzucht, Hohenlieth/Eckernförde
1989	Abschluss Landwirtschaftlich-Technischer Assistent

Studium

1989 – 1996	Grund- und Hauptstudium der Biologie, Carl von Ossietzky Universität Oldenburg
1996	Abschluss Diplom-Biologe Titel der Diplomarbeit: “Auswirkungen landwirtschaftlicher Nutzung auf die Vegetation des Nordender Grodens (Jadebusen) und Konsequenzen für die Brutvögel”

Berufliche Tätigkeit

1996 – 2000	Freiberufliche Tätigkeit für die Nationalparkverwaltung “Niedersächsisches Wattenmeer”, Wilhelmshaven, die Staatliche Vogelschutzwarte im Niedersächsischen Landesamt für Ökologie, Hannover, das Institut für Vogelforschung “Vogelwarte Helgoland”, Wilhelmshaven und die Abteilung “Naturschutz” im NLÖ, Hildesheim
seit 2000	Wissenschaftlicher Mitarbeiter am Institut für Vogelforschung

Ausgewählte Publikationen

Becker, P.H., Thyen, S., Mickstein, S., Sommer, U. & Schmieder, K.R. 1998. Monitoring pollutants in coastal bird eggs. Wadden Sea Ecosystem 8: 59-101.

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Hiermit erkläre ich, dass ich die Dissertation selbstständig verfasst und nur die angegebenen Hilfsmittel benutzt habe.

Wilhelmshaven, Juni 2005

Stefan Thyen