

Conservation of long-distance migratory wader populations: reproductive consequences of events occurring in distant staging sites

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Schekkerman, H., Tulp, I. & Ens, B.J. 2003. Conservation of long-distance migratory wader populations: reproductive consequences of events occurring in distant staging sites. *Wader Study Group Bull.* 100: 151–156.

Many wader species are long-distance migrants using a restricted number of separate sites during their annual journeys. To predict impacts of human activities in one or more of these sites on populations, we need to understand the functional links between sites. Effects carried over from staging to breeding areas are of special interest here, as breeding productivity directly affects population dynamics. Mathematical migration models have been developed which may be used to evaluate such effects. They assume that breeding success depends on the date and the bird's condition upon arrival on the breeding grounds, both of which may be affected by conditions in the wintering grounds and/or along the migration route. Empirical evidence for such relationships has been found, especially in arctic-breeding geese. Similar links are likely to exist for shorebirds, though the mechanisms may be slightly different. We discuss some of the ways in which breeding success of arctic-breeding waders may depend on arrival date and condition. Much work remains to be done in this field, to provide mathematical migration models with the necessary quantitative detail to make them useful as a conservation tool.

LOCAL EFFECTS – WORLDWIDE IMPACTS?

One noteworthy characteristic of waders as a group is that many species are long-distance migrants, using a restricted number of more or less widely separated sites during their annual journeys. Equally characteristic, many of these sites are influenced by human activities that reduce their quality for birds, like reclamation, pollution, disturbance, fisheries or hunting. "Flyways" are networks of sites connecting (and including) breeding and wintering areas, often used by populations of several species simultaneously. Central to the conservation of flyways, as envisaged in international treaties and conventions, is the concept that each site is important in itself, but their functioning is also influenced by the quality of other sites in the chain. For effective conservation, the functional links between sites within these networks need to be understood. Only then can we make ecologically sensible predictions of the impact of human activities on migratory wader populations, and explore whether developing alternative sites could provide sufficient compensation if harmful activities cannot be stopped. Also, knowing for which sites or combinations of sites a reduction in quality would impact most on population size would greatly help prioritise conservation efforts. A flyway approach is also essential if we are to understand the effects of global change, simultaneously affecting many sites along the flyway as well as conditions during flights.

Two main steps must be taken before we will be able to fully understand flyway networks. First, they need to be

"physically" mapped: sites must be identified, and it must be established by which population or part of a population they are used, in connection with which other sites, for what purpose and on which resources their functioning is based. Over the past decades, the local activities of wader students worldwide and international projects by the Wader Study Group and others have contributed greatly to this aspect of our knowledge of wader migrations, though there is still much work to be done. The second step is understanding how the functioning of separate sites is linked to other sites and the flyway as a whole, in terms of population dynamics. Functional links between staging and breeding sites are of special interest here, as it is on the latter that new generations of birds are born to replace those that died on migration or during winter, an equilibrium that determines long-term population size.

In this contribution we focus on the second step. The problem applies to any migratory population, but as arctic-breeding shorebirds undertake longer migrations and are perhaps more time-limited in their breeding cycle than more southern species, we take this group as our example.

MIGRATION MODELS

Making predictions requires a theory. The development of bird migration theory is ably reviewed by Alerstam & Hedenström (1998). During the 1990s, mathematical models describing the migration of individual birds between wintering and breeding areas were developed (Weber *et al.* 1994,

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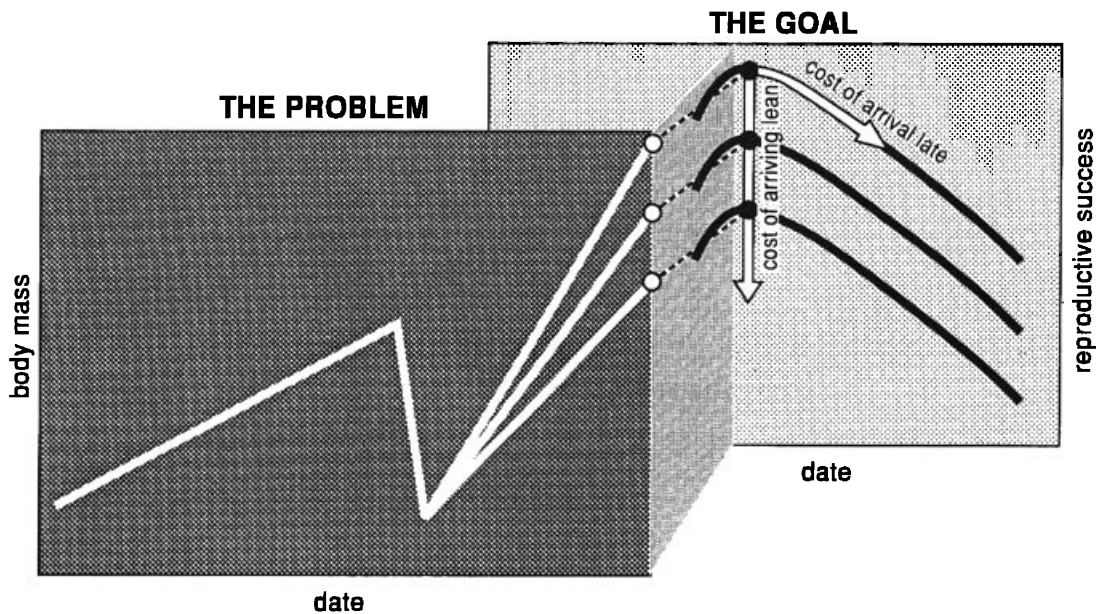


Fig. 1. A graphic illustration of the way in which staging site quality may influence breeding success through differences in fuel deposition rate (from Ens *et al.* 1994).

1998, Clark & Butler 1999, Klaassen 2001) and analysed from a conservation perspective (Weber *et al.* 1999). In these models, the optimal migration strategy is found using stochastic dynamic programming (Mangel & Clark 1988, Houston & McNamara 1999), taking into account characters of the birds (size, flight characters, state-dependency of predation risk), staging sites (rates of energy expenditure and gain, predation risk) and conditions *en route* (wind). It is assumed that the decisions of the birds maximise their fitness. A central point in the models is the relationship between arrival date and arrival condition on the one hand, and breeding success, as a proxy of fitness, on the other (Fig. 1, Piersma & Ens 1992, Ens *et al.* 1994). It is the interplay between this relationship and (mortality) factors operating in the wintering grounds and along the migration routes that determines the optimal strategy and its associated reproductive output. Should a wader that faces a reduced fat deposition rate due to disturbance at its ultimate staging site extend its stay until it reaches "normal" departure mass, or depart with less fuel? And to what extent can the loss of an intermediate site be offset by changing the way in which other sites are used?

The models assume that reproductive success has an optimum with respect to arrival date (Fig. 1), or declines continuously to some final date beyond which reproduction is impossible. Furthermore, some minimum condition is required to initiate a clutch. The shape of this "terminal reward function" is based on general patterns in birds, but will vary between species, localities, and years. From a conservation point of view, it matters much whether breeding output decreases rapidly or only very slowly with arrival date, and whether or not clutch size is a tight function of arrival condition. These are the factors that determine how much leeway there is for birds to tolerate disturbances to the optimal migration schedule. Studying the reproductive consequences of arrival date and arrival condition is thus of great importance to provide an empirical basis for models of migration, and to provide them with the quantitative detail necessary for use as a conservation tool.

STUDIES LINKING STAGING SITE QUALITY TO BREEDING PERFORMANCE

Relationships between events on staging sites and reproductive output have been most clearly shown in the field in arctic-breeding geese. Several characteristics make geese suitable for such studies: wintering areas are often linked to discrete breeding areas, condition can be estimated for large samples using abdominal profiles, marked individuals are easily resighted and frequently reported, and families migrate as units and stay together on the winter grounds. Several species breed (semi)colonially, enabling large sample sizes in breeding studies, which have shown effects of laying date and body condition on reproductive parameters (Ankney & MacInnes 1978, Sedinger and Raveling 1986, Madsen *et al.* 1998, Lepage *et al.* 2000). Brent Geese *Branta bernicla* leaving the Wadden Sea in good condition returned with more young than birds that left in poorer condition (Ebbinge 1989, Ebbinge & Spaans 1995). When farmers on the Vesteralen islands in Norway, a final stopover site of Pink-footed Geese *Anser brachyrhynchus* on their way to Svalbard, started to scare geese off their land, this resulted in poorer departure condition and lower breeding productivity for birds staging in disturbed than undisturbed sites (Madsen 1994). In this species, reproductive consequences of different migration strategies have also been shown (Madsen 1999). Traditionally geese left Denmark relatively late and used the Vesteralen as the only stopover site. New strategies involved the use of Trondheimsfjord. Five different migration strategies were distinguished, varying in departure time from Denmark and the duration of stay at the two sites. Geese using early strategies and using only Trondheimsfjord departed on their final flight in poorer condition and bred less successfully than birds using both sites or only Vesteralen. Strikingly, geese changed their strategy between years in response to breeding success in the previous year: successful breeders used the same strategy, while failed breeders changed to a different one.

Waders lack many of the favourable characteristics of geese. Catching is necessary to establish condition, report-



ing rates are lower, breeding sites are often not known or too extensive to relocate individuals with a known history, and adults and juveniles separate before migration. Studies that directly link stopover site quality to breeding success do therefore not yet exist for waders, but detailed studies of parts of the northward journey can shed some light on possible effects. Gill *et al.* (2002) studied differences between British estuaries in the population increase of Icelandic Black-tailed Godwits *Limosa limosa islandica* over 30 years. At sites with initially low numbers and the steepest increases, godwits showed low foraging success and local survival. Birds using these poor-quality estuaries were shown to arrive later on their Icelandic breeding grounds. However, an effect on their reproductive success remains to be shown.

Other studies have shown consequences of changes in habitat quality at one site due to human interference. Red Knots *Calidris canutus* migrating from their South-American wintering sites to the Canadian Arctic traditionally pass through Delaware Bay on the Atlantic coast of the U.S. After commercial fishing of eggs of Horseshoe Crabs *Limulus polyphemus* started, in recent years fat deposition rates of the staging birds have declined strongly. Over the past three years, the proportion of Knots radiomarked at Delaware Bay that could be relocated during radio-tracking surveys on the breeding grounds declined annually, suggesting that the number actually making it to there declined (L. Niles unpubl. data).

POSSIBLE IMPLICATIONS OF ARRIVAL DATE AND CONDITION IN WADERS

Effects of arrival date and condition on breeding success are likely to vary with the energetic strategy used for reproduction. Many arctic-breeding geese store enough nutrients at their last spring staging site to not only complete the migratory journey, but also produce eggs and sustain (part of) the female's metabolism during incubation ("capital breeders"), although feeding after arrival can also contribute to clutch size (Ganter & Cooke 1996). Under this strategy, arrival condition may directly affect clutch size or the ability of the parent to complete incubation. Recently it was shown that arctic waders produce eggs from nutrients collected after arrival on the breeding grounds ("income breeders"; Klaassen *et al.* 2001). In such a case, condition effects may largely fall parallel with arrival date effects, because birds arriving in poor condition will need more time to acquire the nutrients for a clutch. Nevertheless, it is possible that there is a direct effect of condition on survival during the period immediately after arrival, when food availability is limited and unpredictable due to weather and snow conditions. Unusually cold early summers in 1972 and 1974 seem to have caused extensive mortality of adult Red Knots in northern Greenland and Canada (Boyd & Piersma 2001).

The risk of starvation upon arrival is probably also the greatest potential cost of being early. On the other hand, early arrival may bring several benefits. Early birds may obtain the better territories with respect to food supply or safety. Arrival date may also affect the options to choose a mate, including the chance to re-mate with a known partner, as in the Black Turnstone *Arenaria melanocephala*, where reunited pairs fledged more young than newly formed pairs (Handel & Gill 2000). Early arrival may also translate to an early laying date, although variation in the time needed to accumulate nutrients

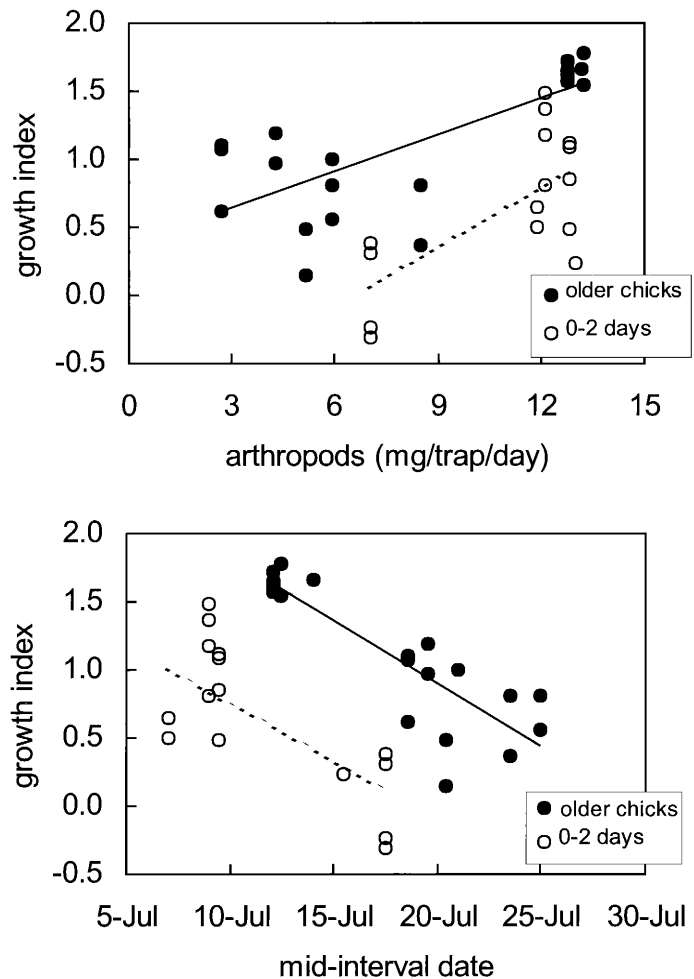


Fig. 2. Growth rate of Dunlin chicks at Medusa Bay, NW Taimyr, covaried with arthropod numbers trapped in pitfalls (upper panel), and declined with date as arthropods became scarcer in July 2001 (lower panel). The growth index is the observed mass increase over a recapture interval divided by the expected increase based on the average growth curve (From Tulp & Schekkerman 2001).

for egg production may modify this relationship. Early arriving birds may fatten up faster if they have access to better feeding sites, though arctic waders often feed outside their breeding territory. However, laying date can also be constrained by a late snowmelt. Eggs can only be laid once suitable nesting ground has become exposed, and nests in small snow-free patches incur a high predation risk (Byrkjedal 1980).

Laying date has been found to be an important component of reproductive fitness in many bird species. Possible mechanisms for laying date effects in arctic waders are:

- **Reduced clutch size.** Some studies of arctic waders have found a negative association between laying date and clutch size (or egg size), either within years (Sandercock *et al.* 1999), or as a reduction in cold years with a late snowmelt (Nol *et al.* 1997, Meltofte 2000). In very late years, birds may forego breeding altogether. However, it is not clear whether these phenomena are caused by some nutritional constraint, or represent an adaptive response to a reduced value of later-born offspring.
- **Food availability for chicks.** Abundance of surface-active arthropods that form the main food of arctic wader



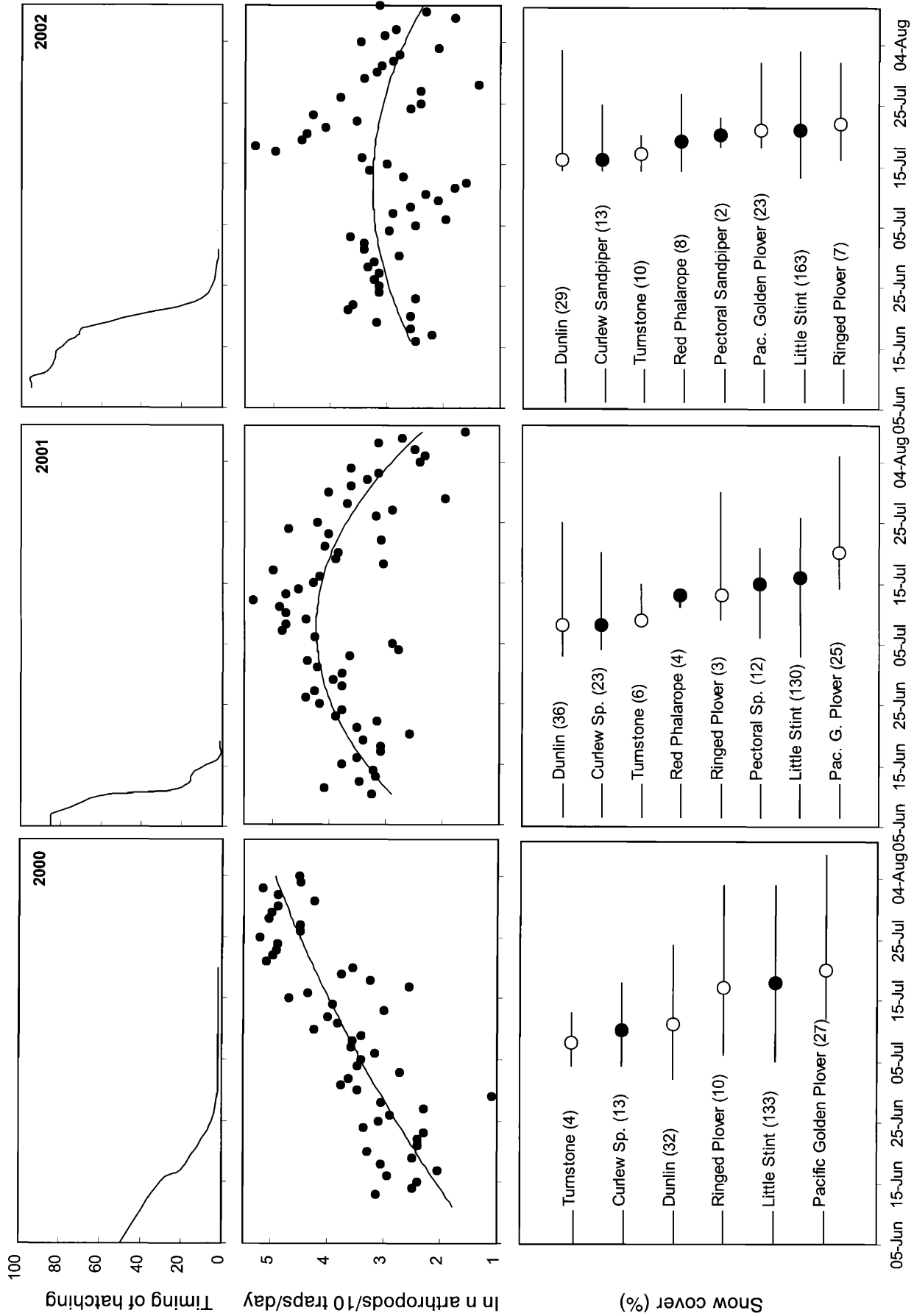


Fig. 3. Snow melt, abundance of surface-active arthropods, and wader hatching dates (dot: median, line: range) at Medusa Bay in 2000, 2001 and 2002. Open symbols represent biparental incubators, closed symbols uniparental species; number of nests between parentheses (L. Tulp *et al.* unpublished).



chicks generally peaks during a short period in (most often) July, the timing of which varies under the influence of weather conditions. A hatching date well-timed to the insect peak will increase chick growth rate and survival (Schekkerman *et al.* 1998, Fig. 2). Although some early authors identified hatching as the phase to be matched with the insect peak (e.g. Nettleship 1973), this may not be the whole story, as required foraging intake rates are higher for older chicks with their greater energy requirements (Schekkerman *et al.* 2003).

- **Food availability for adults.** Although adult waders may utilise a wider food spectrum than chicks (e.g. also buried larvae), food availability for them may also be highest during the peak of surface arthropod activity, and thermostatic costs are low in this period. During incubation, the adults' feeding time is limited, especially in uniparental species which typically only spend 10–20% of the time off their nest. This may lead to a conflict of interest between adults (which could alleviate energetic problems by incubating during the insect peak) and chicks (which should have hatched by then). Possibly as a result of this trade-off, uniparental arctic waders generally breed later than biparental species (Whitfield & Tomkovich 1996).
- **Competition during autumn migration.** In many arctic wader species, one parent deserts the breeding area well before the chicks have fledged, and even the remaining parent usually migrates away before the young. This may reflect a declining food supply in the tundra (less likely for birds deserting after laying), but may also point to some advantage of arriving early at autumn staging or moulting sites. An indication for such an advantage is the study of Boates & Smith (1989), who found that in response to the influx of migrant Semipalmated Sandpipers *Calidris pusilla* into the Bay of Fundy in late July, the larger male amphipods *Corophium volutator* did not show up at the surface anymore due to a behavioural shift and depletion by sandpipers. Thus only the early-arriving birds can take advantage of the most profitable prey. Other studies showing prey depletion at autumn staging sites are Schneider & Harrington (1981) and Szekely & Bamberger (1992).

ATTEMPTS TO MEASURE THE TERMINAL REWARD FUNCTION IN THE REAL WORLD

During the past three years, we have been studying the possible effects of arrival date and arrival condition on breeding success of some wader species in the Siberian Arctic. We have tried a direct approach in that we have caught and marked birds upon arrival on the breeding grounds and successively measured their reproductive parameters (see Smith & Moore 2003 for a passerine example). This has met with limited success, due to problems with capture and estimating fledging success, and complicating factors such as high predation rates. In a more indirect approach we have measured the seasonal pattern of food availability and compared this to energetic demands and performance of parents and young (energy expenditure, condition, growth). If we can pin down energetically stressful periods, it might be possible to identify selection pressures on the timing of breeding. Additional insight can then be gained by comparing the findings

among species that have different reproductive strategies.

Results so far suggest that timing of hatching relative to the peak of surface-active insects is an important factor affecting chick growth and survival. When insect abundance is high, chicks grow faster (Fig. 2). Although the timing of the insect peak is highly variable, chicks grew up on its declining flank in several of the years that we studied them, snow cover early in the season often preventing a better match (Fig. 3 and data from 1994 and 1996). This points to a general advantage of breeding as early as possible, but how steep the seasonal decline in reproductive value is, is not yet clear. It is noteworthy that even at 73°N species like Dunlin *C. alpina*, but also Pacific Golden Plover *Pluvialis fulva* with a relatively long breeding cycle, can replace lost clutches until some three weeks after the median laying date of first clutches. In the double-clutching Little Stint *C. minuta*, laying dates span a similar interval. However, we do not know to what extent late-hatched young make it to staging and wintering areas.

WORK FOR THE FUTURE

To further improve the usefulness of migration models for the conservation of migratory waders, we need more studies giving insight into the shape of the terminal reward function. Data from existing as well as new research can be analysed from this point of view, and temperate-breeding waders may prove just as interesting as arctic species. Studies using marked individuals and spanning several years will be especially valuable, as they may give insight into the confounding effects of individual quality. For instance, a correlation between arrival date and breeding productivity between individuals could be a direct causal effect, but might also result from birds that are intrinsically "better" at migrating also being better in some aspect of reproduction. Looking at intra-individual variation is one way to circumvent this problem. The ultimate challenge will be to design and carry out experiments in which condition and arrival or laying date are manipulated, e.g. by taking birds into temporary captivity or by supplemental feeding. A second major challenge is studying effects of hatching date and fledging condition on post-fledging survival and recruitment, a topic that we as yet know very little about in waders compared to some other bird groups.

At present, the DYNAMIG model simulates the spring migration of individual birds. To make it a more useful conservation tool, it should be extended to a year-round model, and ideally also include competition between individuals (density dependence, depletion effects, i.e. the advantage of arriving before competing conspecifics). Only then will we be able to predict the consequences of human impacts on the population dynamics of migratory waders.

ACKNOWLEDGEMENTS

Our studies are funded by the Dutch Ministry of Agriculture, Nature Management and Fisheries (DWK program 404). Hans Meltote provided helpful comments on the manuscript.

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