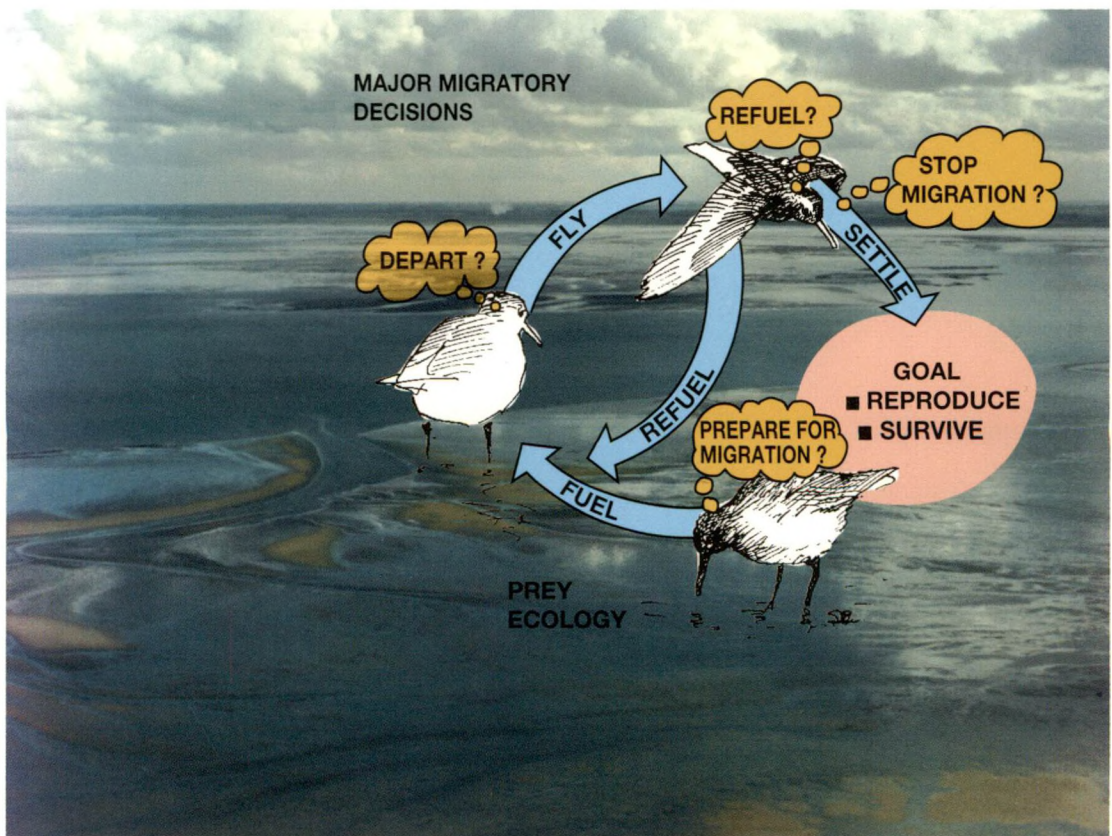


TOWARDS PREDICTIVE MODELS OF BIRD MIGRATION SCHEDULES: THEORETICAL AND EMPIRICAL BOTTLENECKS

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NETHERLANDS INSTITUTE FOR SEA RESEARCH

PREFACE

A few words on how this meeting came about and what made it possible may be of interest. The idea for the meeting arose during a visit to Oxford. The combined presence of Peter Hicklin and BE prompted Alasdair Houston to organize a small meeting to discuss models of migration. This impromptu meeting was also attended by Richard Caldow, John McNamara, Tony Moodey, Bill Sutherland, Thomas Weber and Wolfgang Weisser. In part because the meeting worked so well, it seemed that more people could have profited from attending. Also, the discussions might have been even more lively with a somewhat greater audience and a greater share of die-hard empiricists, willing to harp on every possible weakness in the models. Finally, there was a feeling that the study of migration strategies was rapidly gaining momentum and that this provided an important window of opportunity to forge a link between the empirical and theoretical studies of migration and thereby set them on a common course. Phoning around made it clear that many people were happy to attend such a "theoreticians-meet-empiricists" meeting. Initially envisaged as a small meeting of at maximum 35 scientists it grew to a meeting of almost double that size through word of mouth in combination with a deliberate policy to let enthusiasm have its way. Wim Wolff showed great enthusiasm at the first mention of the idea and helped to organize funds. These funds were used to pay for the travel expenses of some dearly wanted participants, mainly from the other side of the Atlantic, and for the publication of this report. Without the willingness of the majority of the participants to pay for their own expenses, the meeting would not have been possible though. Funds were obtained from the National Research Programme on Global Air and Climate Change, the Institute for Forestry and Nature Research and the Netherlands Institute for Sea Research. The cooperative attitude of Joke Hart, Michaela Scholl and Gjalte Steenhuizen during the meeting substantially contributed to its success. We are also grateful for the many replies that we received to our request for comments on an earlier version of this report. Comments were received from: Thomas Alerstam, Herbert Biebach, Bruno Bruderer, Dan Cristol, Peter Evans, John Goss-Custard, Anders Hedenström, Richard Holmes, Alasdair Houston, Lukas Jenni, Susi Jenni-Eiermann, Marcel Klaassen, Felix Liechti, Åke Lindström, Jaap van der Meer, Frank Moore, Martin Morton, Berry Pinshow and Thomas Weber. Especially gratifying were the comments of Ellen Ketterson, a participating non-participant, and the long letters of Paul Dolman, full of healthy disagreement. Henk Hobbelink enthusiastically engineered a cover for this report. The report was produced by Anneke Bol and Nelleke Krijgsman.

TOWARDS PREDICTIVE MODELS OF BIRD MIGRATION SCHEDULES: THEORETICAL AND EMPIRICAL BOTTLENECKS

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"The relation of theory to experiment in biology has been an uneasy one. The word 'theoretical' has generally had perjorative connotations, and the right to theorize was the reward for years of laboratory and field work. In fields where progress depends mostly on the refinement of technique in order to facilitate more accurate description, this perhaps did not matter too much, but other areas suffered from an indigestion of facts, while data was collected without reference to problems. In these circumstances, theoretical work often diverged too far from life and became exercises in mathematics inspired by biology rather than an analysis of living systems."

(LEVINS, 1968)

INTRODUCTION

Take the archetypal wader, breeding on the arctic tundra, using intertidal mudflats in the temperate zone as a stopover site during migration and wintering on intertidal mudflats in the tropics. What will happen to the birds if some of their habitats are modified by man for exploitation, like reclamation of the intertidal mudflats or oil-drilling on the tundra? Desired answers would almost certainly include expected changes in the number and timing of birds using the affected areas, as well as changes in their pattern of mass gain. It will not be easy to give such answers. It will be even more difficult to predict what will happen if all habitats are simultaneously affected by global climate change. One way to go about answering these questions is to treat them as thought experiments where our ability to come up with an answer indicates the current state of our knowledge. So, what is the current state of our knowledge?

There is no doubt that studies of the migratory movements of birds have a long history. Although early students of migration did not fail to theorize (see review in GAUTHREUX 1982), attempts to construct formal mathematical models, a necessary prerequisite for precise predictions, are of much more recent origin. In the late sixties and early seventies PENNYCUICK (1969) and TUCKER (1973) presented basic flight mechanical theories about bird migration. In the seventies formation flight and wind effects were evaluated (PENNYCUICK 1978, ALERSTAM 1979). In the eighties game theory (see MAYNARD SMITH 1982) was used to study the conditions for partial bird migration (LUNDBERG 1987) and stable geographical population segregation (LUNDBERG & ALERSTAM 1986). In the nineties simple optimization procedures were used to predict optimal departure fat loads (ALERSTAM & LINDSTRÖM 1990). In addition increasing use is being made of stochastic dynamic programming to handle more complex dynamical aspects of migration. The usefulness of this mathematical technique in the study of foraging and life history problems was

brought to the fore by MCNAMARA & HOUSTON (1986) and MANGEL & CLARK (1986). As the original flight mechanical theories were also continually improved and added upon throughout this period (RAYNER 1988, PENNYCUICK 1989), there can be no doubt that mathematical models that account for the various aspects of migration are developed at an increasing rate.

Although this is a healthy development, there is a risk that the theoreticians will become so excited by each other that they disappear en masse into outer space, instead of confronting the more empirically minded students of migration with penetrating questions. Such questions can be of great help in warding off the ever-present danger of drowning in the complexities of nature. In return, theoreticians will profit from remaining anchored to the real world, even though it may be profoundly irritating to be told the facts of life by members of the scientific community with mud on their boots. Using more deferential language it amounts to the conviction that scientific progress is hampered when theoretical advances are not accompanied by comparable advances on the empirical side of the research program. Only through close cooperation will it be possible to achieve advances on both sides. A clear example of what may go wrong is niche theory, which sought to explain the patterns in animal communities as a result of interspecific competition (MACARTHUR 1972). While theory became increasingly complex, insufficient advances were made in the development of a methodology that allowed the actual measurement of limiting resources in the field. As a result, the research program was not proven wrong or substantially modified on the basis of empirical evidence, but simply abandoned by the mainstream of ecologists.

It is therefore to be hoped that the workshop, organized on Texel from 6 to 8 July 1993, succeeded in establishing firm links between theoreticians and empiricists, through the direct confrontation of ideas with facts and vice versa, as well as through the establishment of personal contacts. Despite the large

number of participants the meeting retained its intended informal character. Though discussions were lively, participants spent their energy in exchanging ideas instead of display behaviour intended to impress, or claim priority. This suggests that close personal contacts are a remedy against the trend noted by MADDOX (1993) that intensifying social competition among scientists is increasingly crippling science through impeding the free flow of ideas. The remedy relies on the observation that scientists, like other animals, cannot escape being prisoners of their social relationships. Since limits to the time budget of an animal will limit the time available for social contacts, the number of sufficiently intimate relationships will be limited too, suggesting that the remedy does not work when the number of scientists is too large.

DEFINING THE PROBLEM

Birds are only capable of completing a full migratory cycle if they possess formidable powers of navigation. No wonder that much research effort has concentrated on trying to understand the mechanisms of navigation (PAPI & WALRAFF 1982). Similarly, successful completion of the migratory cycle requires a proper timing. Mainly through the work of GWINNER (e.g. 1990) experiments with migratory birds have provided some of the best demonstrations of the existence of endogenous circannual rhythms synchronized by environmental zeitgebers. However, an understanding of some of the abilities that allow birds to make their migratory journeys is a far cry from a theory predicting the details of a migration schedule of a particular bird species (PIERSMA 1987, ALERSTAM & LINDSTRÖM 1990, ENS *et al.* 1990).

BAKER (1978) formulated a very general model and couched it in such abstract terms that it remains "unfamiliar to most" according to KETTERSON & NOLAN (1983). These authors subsequently state that "while the comprehensiveness of the model makes it admirable in the abstract, in practice it may render predictions untestable". The alternative to constructing a very general and comprehensive theory encompassing all possible types of movement in the entire animal kingdom is to build models for well-defined and therefore necessarily limited problems. This was more or less the approach implicitly or explicitly taken by the participants of the workshop. Like BAKER (1978) it was generally assumed though that the details of a migration schedule are shaped by natural selection.

The fact that at present none of the participants seemed to be constructing a grand unifying theory should not be taken to mean that such a theory is not wanted. In contrast, an important goal of the workshop was to identify how the various studies of specific migratory decisions fit together. After all, there can be no doubt that solutions to one problem con-

strain the possible solutions to other problems. To avoid misunderstandings it is important to make clear that in this report the word decision is used in the sense of MCFARLAND (1977) for cases where several mutually exclusive behavioural options exist for the animal: "there must be some process or mechanism that determines which activity is to have priority at any particular time, and such a process is conveniently termed a decision process". Thus, the use of the word decision is in no way intended to imply conscious choice by the animal. Figure 1 depicts an idealized decision scheme of a migratory bird. The simplicity of the scheme effectively hides the many discussions between the three of us during its gestation. According to the scheme the migratory journey of an individual bird can be broken down into four major decisions: (1) the decision to start preparations necessary for migration like building up fuel stores, (2) the decision to depart on the migratory flight, (3) the decision to interrupt the migratory flight for refuelling and (4) the decision to end migration altogether and search for a good site to breed or survive the non-breeding season. These decisions lead to one of three phases: the fuelling phase, the flight phase and the resident phase. During each phase continuously a multitude of decisions has to be made in response to the prevailing conditions in order to reach the appropriate state characterizing the phase. During the fuelling and refuelling periods the animal has to decide on the rate of mass gain in response to local food conditions and predation risks. During the migratory flight the animal has to decide on the position in the flock, the flight speed and the flight altitude in response to the weather conditions en route. Finally, the bird has to settle down, taking habitat quality and the presence or absence of competitors into account.

The scheme has broken down the problem into a set of decisions, allowing an enquiry into the costs

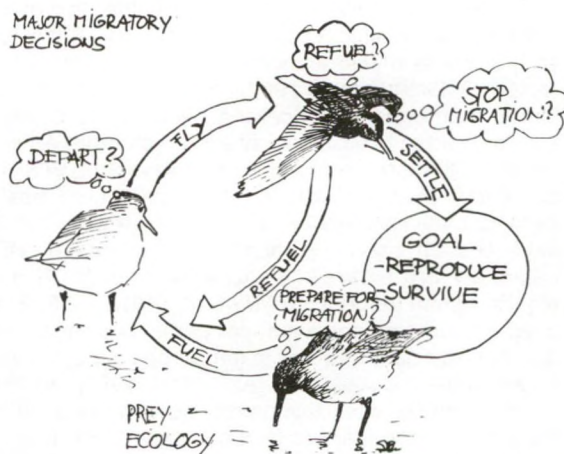


Fig. 1. Idealized scheme of the major migratory decisions faced by a migrating bird (see text for a detailed discussion).

and benefits (which must ultimately be expressed in terms of fitness), as well as the underlying mechanism of each decision. At the same time the scheme highlights the interdependence of the decisions: though the various decisions may be studied as independent problems in their own right, the final solution requires that the results of these studies fit in the same frame. What the scheme does not depict is the directional component of some of the decisions. Apart from deciding what to do when, the animal must also decide where to go. Furthermore, though the scheme presents the problem as one of the individual bird facing a sequence of behavioural decisions, reference to a lower level of integration, i.e. physiological processes inside the animal, and a higher level of integration, i.e. population processes, will be necessary. Physiology for instance, determines how far a bird can fly with a given fat load at a given wind speed, while the costs and benefits in terms of fitness of a particular migratory decision will often depend on the migratory behaviour of conspecifics, i.e. on population processes. In fact, instead of describing the migration schedule as being adhered to by a hypothetical single individual many of us ultimately want to include the number of individuals in the description of a migration schedule.

THE MIGRATORY FLIGHT

FLIGHT MECHANICS

Flight mechanics is a basic element in theories of bird migration (ALERSTAM 1991). A central element of flight mechanics is the power curve, which predicts that energy expenditure will be high at both low and high flight speeds and reach a minimum at intermediate speeds (PENNYCUICK 1989). This power curve can be used to find the flight speed that minimizes the energy cost per unit time, the flight speed for minimizing the energy costs per unit of distance covered (the maximum range speed) and the optimal flight speed for minimizing the total duration of the migratory journey (Fig. 2). ALERSTAM *et al.* (1993) observed for a range of seabirds that average airspeeds fell between the minimum power and maximum range speeds estimated from aerodynamical theory. BRUDERER & WEITNAUER (1972) showed that Common Swifts remain airborne during sleeping flights at about the theoretical speed of minimum power and closely

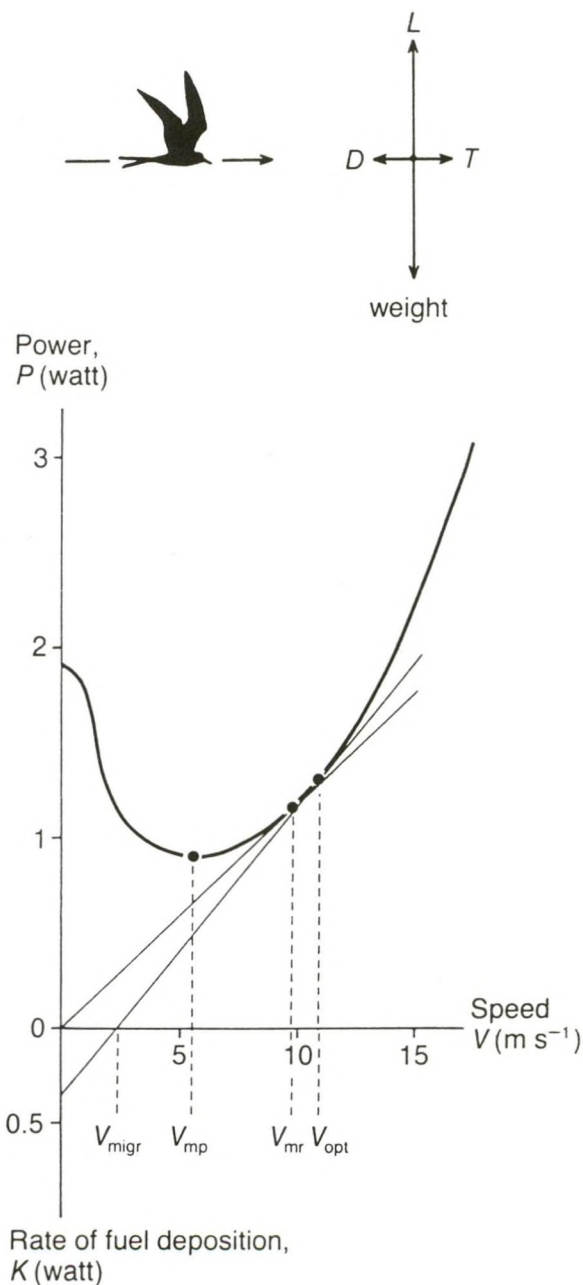


Fig. 2. Power curve estimated for the Arctic Tern according to the theory of bird flight mechanics. The mechanical power output indicated on the power axis should be divided by the conversion efficiency (normally assumed to be about 23%) to give the total chemical energy metabolized by a flying bird. The rate of fuel deposition is converted into its mechanical equivalents to be compatible with the flight power given. V_{mp} is the speed that minimizes energy costs per unit of time. V_{mr} is the speed that minimizes the energy costs per unit of distance covered. V_{opt} is the optimal flight speed for minimizing the total duration of a migratory journey, including the periods of fuel deposition. V_{migr} is the maximal overall speed of migration that can be attained. From ALERSTAM (1991). Reprinted with permission from Elsevier Tredn Journals.

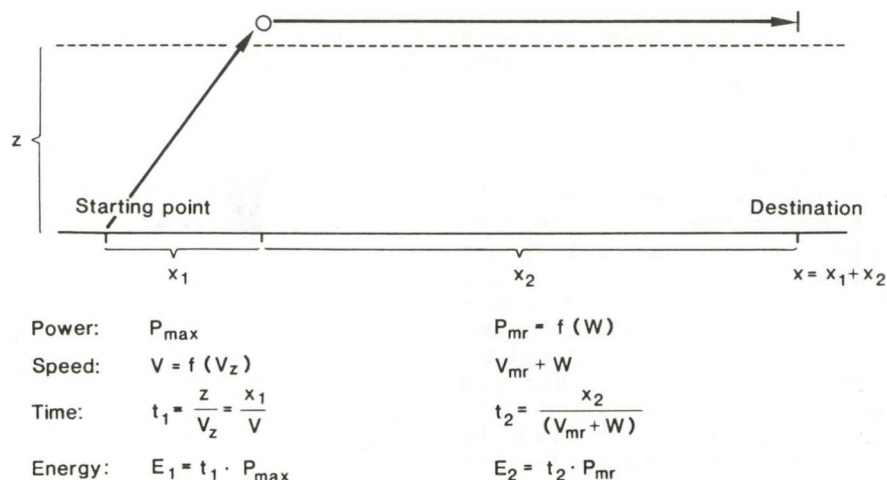


Fig. 3. Schematic migration flight with an initial climbing phase to altitude z when distance x_1 is covered and a cruising phase when distance x_2 is covered. We have indicated the qualities needed to derive the total energy cost ($E_1 + E_2$) for the entire migration flight, which is the currency being minimized with respect to climb rate (see HEDENSTRÖM & ALERSTAM, 1994 for details)

match maximum range speed during migratory flights. LIECHTI (1992) showed that small passerines adjust their airspeed to wind conditions in close agreement with the theoretical curve.

Anders Hedenström applied the power curve to calculations on climbing flight. A simple model predicting the optimal rate of climb for birds setting out on a migratory flight was presented (Fig. 3). The model uses an energy minimization argument for the entire flight (climbing and cruising phases) and gives the climb rate resulting in minimum cost of transport. Some data in support of the model was presented of shorebirds departing from NW Iceland during spring migration (HEDENSTRÖM & ALERSTAM 1994). Comparing species, a negative relation between climb rate and body mass was predicted, and observed. A negative correlation between maximum fuel load capacity, i.e. the fuel load at which climbing flight is still possible, and body mass was also predicted and observed. As the maximal flight range is determined by the maximal fuel load capacity it follows that potential flight ranges are size-dependent (HEDENSTRÖM & ALERSTAM 1992).

Bruno Bruderer (in press) reported on the first study combining on-site radio sonde measurements with reliable radar observations on height distribution of migrants crossing the Negev desert in Israel. In addition, the data were gathered under extreme temperature and humidity conditions, and by this, enabled Bruderer and co-workers to test existing hypotheses on the influence of temperature and humidity on altitude distribution. A statistical model, developed in cooperation with Les Underhill (BRUDERER *et al.* in press), indicated that choice of height

stratum was primarily affected by the amount of tail wind, contradicting suggestions (see later) that nocturnal migrants above desert areas have to adjust their flight level to minimize evaporation of water. The model, which assumes that the birds compare the meteorological conditions in the adjoining height strata and then switch to the more profitable layer with a certain estimated probability, yielded a close fit to the empirical data: the change in tailwind speed predicted on average 63% of the autumn and 56% of the spring distributions, while none of the other variables had a significant influence. Fig. 4 provides an example.

Felix Liechti combined the model of PENNYCUICK (1969, 1989) for maximum range speed with ALERSTAM's (1979) model on optimal drift strategy, calculating the optimal adjustment of heading and airspeed to compensate for changeable winds with respect to a specific goal (LIECHTI 1992, 1993 and in press). In this case flying the maximum range is regarded optimal (Fig. 5). Under most wind conditions the proposed statistical model on optimal behaviour came close to the observed behaviour, but large deviations from the model occurred under strong side winds (above 5 m/s).

ENERGY AND OTHER POTENTIALLY LIMITING RESOURCES DURING MIGRATION

Under the assumption that only energy is critical, maximal flight range can be calculated for a given fat load from the previously discussed power curve. However, the assumption may be wrong. There may be conditions (i.e. ambient temperatures) where

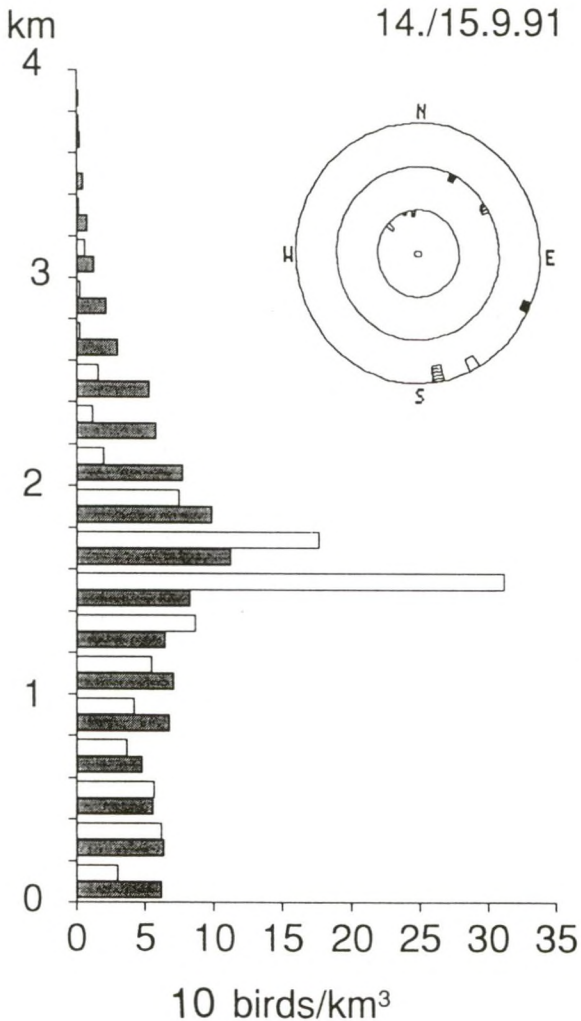


Fig. 4. Comparison of predicted (shaded bars) and observed (white bars) height distribution of nocturnal bird migration in autumn (14/15.9.1991) over the Arava Valley (Israel). Predictions are based on the difference in tailwind between neighbouring height levels. The circular diagram in the upper right corner indicates the wind direction and speed (length of the bar) for three height intervals (inner circle 0 to 1000; middle 1001 to 2000; outer 2001 to 3000 m above ground level) and throughout the night (white 20:00 h, black 24:00 h, shaded 4:00 h). From BRUDERER *et al.* (in press).

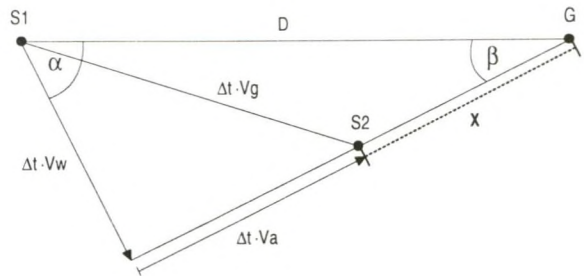


Fig. 5. Optimal flight behaviour: minimizing energy expenditure during one flight stage in relation to a specific goal. The distance flown in one stage ($\Delta t \cdot V_g$) is the sum of the work done by the bird ($\Delta t \cdot V_a$) and the displacement by the wind ($\Delta t \cdot V_w$). For an optimal behaviour the remaining distance after the flight stage (X) must be minimal. (S1=starting point, S2=stopover site, G=goal, D=initial distance to the goal, α =wind direction, β =direction of heading, V_a =airspeed, V_w =wind speed, V_g =groundspeed, Δt =flight time). From LIECHTI (1992).

water loss, instead of energy expenditure, limits flight range (YAPP 1962, BIESEL & NACHTIGALL 1987). In a recent model CARMÍ *et al.* (1992) have sought to quantify these conditions. Marcel Klaassen (in press) subsequently refined the model of Carmi *et al.* with respect to the feedback of the difference between metabolic water production and total water loss (i.e. net water loss) on the flight costs. The flow chart of the modified model is presented in Fig. 6.

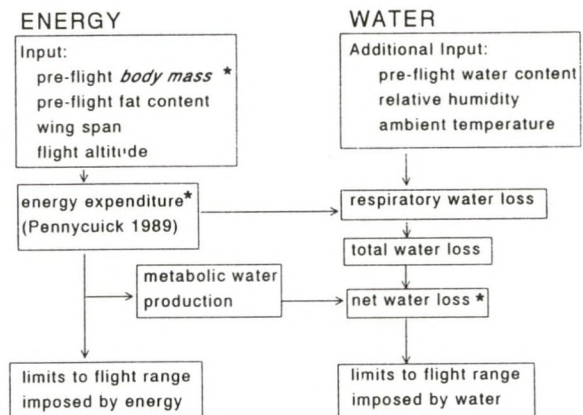


Fig. 6. Flow chart of the physiological processes underlying the computer model of CARMÍ *et al.* (1992) and including the refinement of KLAASSEN (in press). Since the bird loses mass continuously during the flight the program performs iterations over small time steps. The variables affected by the refinement of KLAASSEN (in press) are indicated with a *.

When meteorological conditions are known, the water loss model, which necessarily includes a calculation of the energy balance, allows the prediction of the flight altitude that maximizes flight range. Radar observations by Biebach and Klaassen on migrants crossing the Egyptian desert showed that observed flight ranges corresponded more closely to the predictions from the water loss model than to the predictions from the energy balance model alone. The water loss model also predicts that flight range can be increased by interrupting the trans-Sahara flight during the day. Analysis of radar observations on the patterning of the passage of migrants at different locations by Herbert Biebach indicates that many migrants do indeed rest during the day, as suggested by BIEBACH *et al.* (1991). Further support for such interruptions was provided by the observations with tracking radar of BRUDERER *et al.* (in press). However, since in Bruderer's data on migrants crossing the Negev desert the birds did not adjust their flight levels

according to the temperature or humidity profile, they did not seem to be limited by water loss (BRUDERER *et al.* in press).

Though the water loss model has met some empirical success it was generally agreed that many important parameters and processes were poorly known. The following two questions were identified as the most burning: (1) how much water can a bird lose before suffering physiological damage, (2) what is the rate of water loss under various conditions? Given that, apart from energy, the water balance may sometimes be crucial in determining flight range, it was felt that it might pay to take an even broader perspective and also consider the role of protein turnover and the need for sleep. In fact, there was a general consensus that fat, protein and water constituted a complex of components potentially limiting the migratory flight.

THE MIGRATORY JOURNEY: (RE)FUELLING, DEPARTING AND FLYING

In the above we have discussed decisions that need to be made during the flying phase. In the following we will discuss decisions and physiological adaptations during the fuelling phase alone, or in combination with the flying phase.

PHYSIOLOGY OF MAKING AND USING NUTRIENT STORES

Lukas Jenni reported on his physiological studies on migrant passerines caught when crossing the Alps (JENNI-EIERMANN & JENNI 1991, JENNI & JENNI-EIERMANN 1992). Measurement of the plasma level of triglycerides (the form in which fat is normally transported to the adipose tissue) suggests that small passerines resynthesize triglycerides in order to achieve a high rate of fat utilization during migration. This hints at an additional metabolic pathway not normally used by mammals during exercise (JENNI-EIERMANN & JENNI 1992; Fig. 7). Furthermore, day migrants seemed to rely less on fat compared to night migrants. Thus, it appears that differences in metabolic physiology are closely linked to the migratory strategy of a species.

SUSI JENNI-EIERMANN & JENNI (in press) showed that plasma triglyceride levels in the blood of birds during stopover can be used to predict the amount of mass change, i.e. the amount of fat stored, during that day. This allowed them to conclude on the basis of measurements on birds caught only once that insectivorous birds store less fat during days when feeding conditions seem poor, i.e. after rainfall and at high wind speeds (JENNI & JENNI-EIERMANN unpublished). This biochemical technique may prove a powerful tool for evaluating strategies of fuel storage in the field as it circumvents many of the estimation problems discussed by ZWARTS *et al.* (1990).

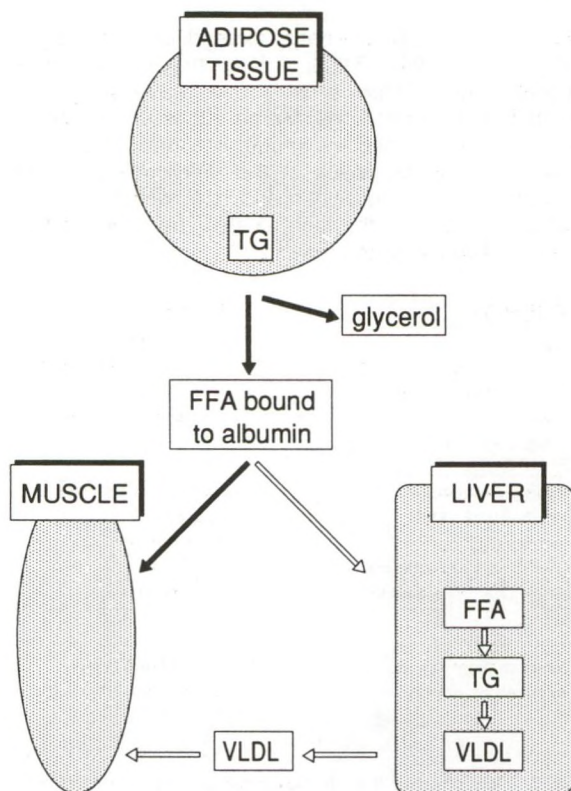


Fig. 7. Simplified model of fatty acid transport from adipose tissues to the muscles. Black arrows indicate the usual pathway. Double-lined arrows indicate the pathway, which is suggested to help to increase fatty acid delivery to the flight muscles during flight in small migrants. FFA = free fatty acids; TG = triglycerides; VLDL = very low density lipoproteins. Based on JENNI-EIERMANN & JENNI (1992).

CONSISTENCY IN ALLOMETRIC RELATIONSHIPS OF PHYSIOLOGICAL AND ECOLOGICAL VARIABLES

Jaap van der Meer, in collaboration with Theunis Piersma, had embarked on an evaluation of various allometric relationships between a dimension of body size and variables like maximal intake rate, energy expenditure during resting and foraging and energy cost of thermoregulation. When these allometric relationships are formalized in a consistent manner, it can be investigated in what way the shape of some selected relationships constrain the shape of the other relationships, assuming the animal retains energy balance. It is also possible to enquire into the conditions under which maximum fat deposition rate shows a negative correlation with lean body mass, as reported by LINDSTRÖM (1991).

OPTIMAL DEPARTURE FAT LOADS

All models that seek to explain departure fat loads as optimal decisions necessarily include assumptions about the flight phase. The marginal value, with respect to flight distance, of adding an extra gram of fuel will decrease with increasing fuel loads due to the increased flight costs. From this the optimal departure fat load can be calculated for a given fat deposition rate and a given optimization criterion (Fig. 8, ALERSTAM & LINDSTRÖM 1990). Possible criteria are minimizing the time spent on the migratory journey, or minimizing the energy spent on covering a given distance. Though the positive relationship between departure fat load and fat deposition rate predicted by the time minimization hypothesis was found in a field experiment with Bluethroats, the observed departure fat loads remained below the predicted levels (LINDSTRÖM & ALERSTAM 1992). This could be due to not all individuals having the same expected speed of migration, or to variations in the expected speed of migration along the migration route.

Assuming that increasing fat loads increase the risk of predation, smaller departure fat loads are also expected when birds attempt to maximize safety from predation during the migratory journey (ALERSTAM & LINDSTRÖM 1990). Experiments by Åke Lindström to test if captive Chaffinches and Bramblings would put on less fat when regularly confronted with a model Sparrowhawk yielded mixed results.

Crucial for the theory developed by ALERSTAM & LINDSTRÖM (1990) is a time or energy cost during a settling phase preceding fat deposition in a stopover site. During the discussions it was questioned if such a phase really exists. The study of Frank Moore on a barrier island (see MOORE *et al.* 1990) where migrants are caught upon arrival and immediately followed using telemetry, seemed ideally suited to obtain the necessary insights on this settling phase. The model of Alerstam and Lindström is most applicable to birds that migrate over areas where suitable

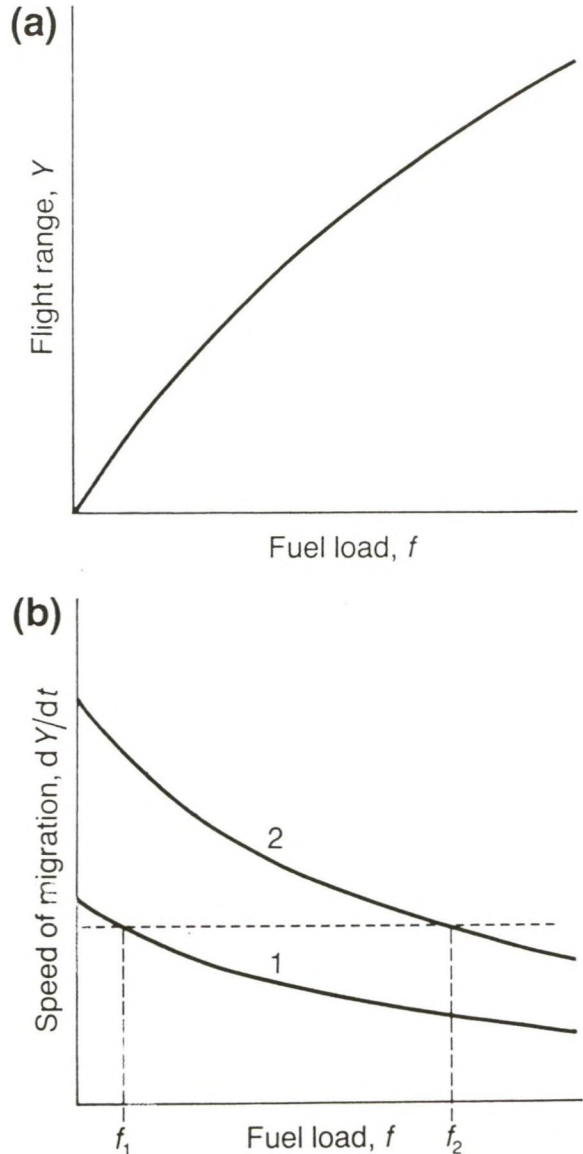


Fig. 8. Prediction of optimal fuel loads. (a) The relationship between flight range (Y) and fuel load (f) at departure will be negatively accelerated because of increased flight costs with increasing fuel loads. (b) As a consequence the marginal rate of gain in potential flight distance (dY/dt) for a bird maintaining a constant rate of fuel deposition on stopover will drop as the bird attains progressively larger fuel loads (f). This relationship is shown for a low-quality (1) and high-quality (2) stopover site. Given an expected speed of movement along the migration route according to the horizontal broken line, the optimal fuel load for maximizing speed of migration is f_1 for departure from the poor site 1, and f_2 for departure from the high quality site 2. From ALERSTAM (1991). Reprinted with permission from Elsevier Trend Journals.

habitat is more or less widespread, as may be the case for most passerines. GUDMUNDSSON *et al.* (1991) show how the idea of time minimization must be applied when only a few, discrete, stopover sites are at hand, which probably is the case for many wader and waterfowl species. When a good knowledge exists of the conditions at various potential stopover sites (which is rarely the case), detailed predictions about a complete migratory journey can be derived.

OPTIMAL RETURN JOURNEY

The expectation that the speed of migration, or some other parameter characterizing migration, is optimized, derives from the belief that migration is shaped by natural selection. Yet, natural selection maximizes fitness. Thus, it would be nice if it was possible to evaluate the fitness consequences of migratory decisions directly. This is exactly what Fig. 9 does by proposing that to each combination of arrival date and arrival mass a fitness value can

assigned. Building on the knowledge on flight costs and the physiology of fuel storage discussed above, the technique of stochastic dynamic programming (MCNAMARA & HOUSTON 1986, MANGEL & CLARK 1986, MANGEL & CLARK 1988) then allows us to find the optimal decisions concerning mass gain and departure for the return journey. Thomas Weber showed the first results of such an analysis. When stochasticity was made to increase along the migration route, the last staging site was sometimes skipped. Perhaps not surprisingly, departure weights exceeded the weight necessary to reach the next stopover site when there was stochasticity in the expenditure during flight over a given distance. It may be possible to estimate the extent of this stochasticity from data on Knots which encounter quite variable wind conditions between years when migrating from the Banc d'Arguin to the Wadden Sea in spring (PIERSMA & VAN DE SANT 1992). In unfavourable years many birds were apparently forced to use an intermediate stopover site, while arrival in the Wadden Sea was delayed.

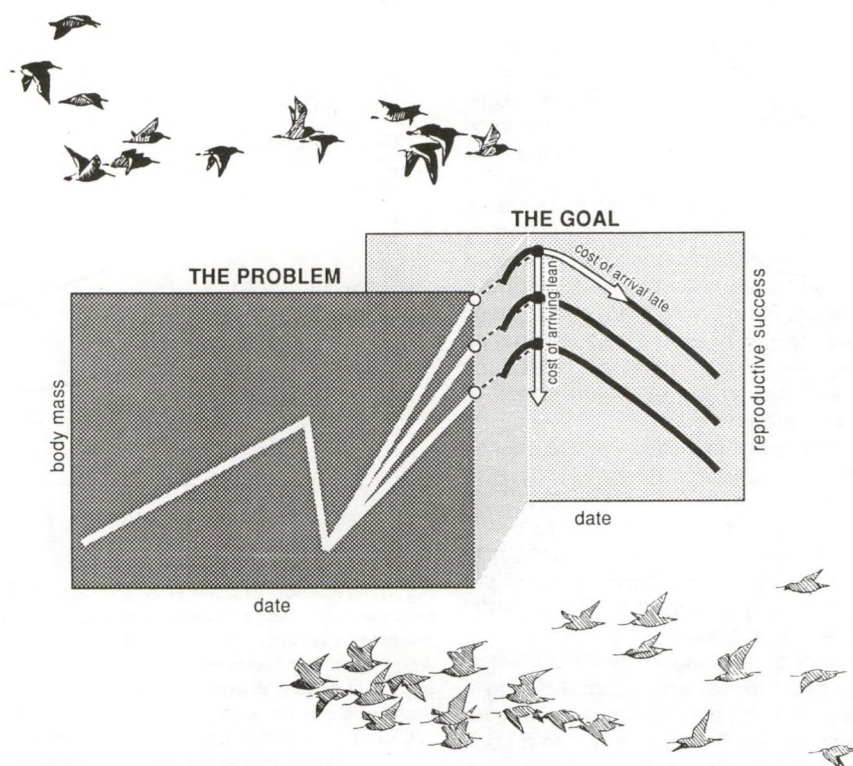


Fig. 9. Schematic presentation of the link between the ultimate goal (maximizing fitness, in this case equated to reproductive success on the breeding grounds) and the problem of how mass gain should be patterned during spring migration (based on PIERSMA & ENS 1992).

OPTIMAL DECISIONS AND STOCHASTICITY

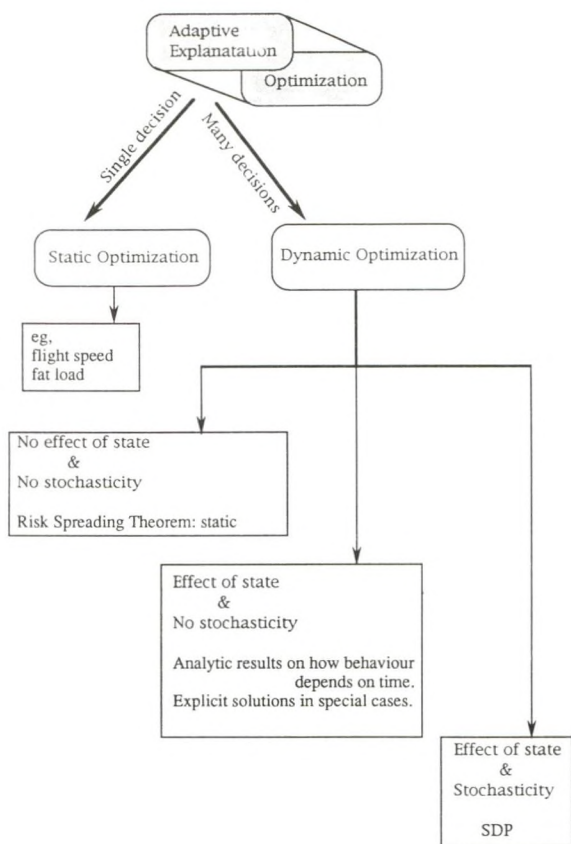
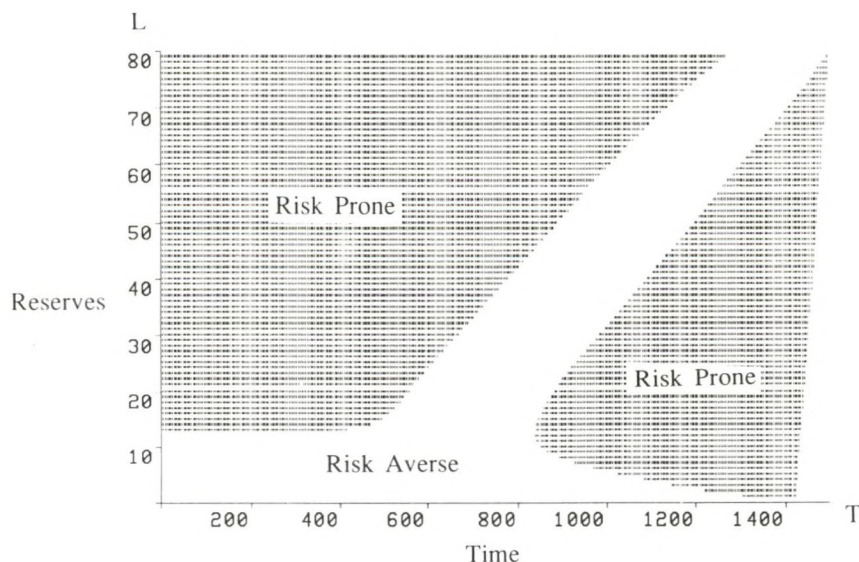


Fig. 10. Diagram depicting the conditions under which different types of optimization models are most appropriate (Alasdair Houston).

Of course, stochastic dynamic programming is not without its problems either. The technique is non-analytic and often involves many parameters. This makes it hard to understand the exact causes as well as the generality of the simulation results. Alasdair Houston used his work on the trade-off between gaining energy and avoiding predation to discuss the conditions under which different types of models were most appropriate to problems of dynamic optimization (HOUSTON *et al.* 1993). When an effect of state (e.g. fat load) is present and stochasticity is negligible, analytic solutions can often be found. However, when the foraging environment is stochastic, simple analytical models are most likely to fail and stochastic dynamic programming seems the only theoretical avenue (e.g. HOUSTON & McNAMARA 1993). The various possibilities are depicted in Fig. 10. A striking example was on the buildup of fat stores prior to migration in a variable environment. At low reserve levels risk averse behaviour, meaning preference of a smaller variance in intake rate at a same mean, is expected when the latest possible departure date is still a long way off, but it switches to risk prone behaviour, i.e. preference of a higher variance in intake rate at a same mean, either if reserves are higher or if the time until departure is reduced (Fig. 11, BEDNEKOFF &

Fig. 11. Graph showing for each combination of reserve levels (maximum 80) and time steps before final time T whether a hypothetical migrant birds should be either risk prone (preferring a high variance in intake at a same mean) or risk averse (preferring a low variance in intake at a same mean). In the model final time T represents the last opportunity to migrate effectively. Successful migration is only possible with maximum reserve levels. Simulations are based on model 2 (pre-migratory fattening under predation hazard) of BEDNEKOFF & HOUSTON (in press).



HOUSTON in press). Laboratory experiments by MOORE & SIMM (1986) demonstrate risk prone behaviour in a migrating bird. Indeed, it may well be that migrating birds offer excellent opportunities for the study of the risk proneness of foraging behaviour, since the penalty is not death, but delayed arrival, or the skipping of a breeding season. That is to say, migration offers a situation where risk-prone behaviour can be advantageous without death being very likely. LORIA & MOORE (1990) and MOORE (1992) demonstrated differences in foraging behaviour between fat and lean migratory birds in field studies on a stop-over site. The next challenge consists of actually measuring that the observed foraging behaviour is risk prone or risk averse.

Enormous environmental stochasticity was apparent in the study by Martin Morton of the Mountain White-crowned Sparrow. On the same date the breeding grounds were sometimes covered by several meters of snow, or no snow at all, depending on the year. For every 2 days delay in breeding, due to snow conditions at the start of the season, there was a 1 day delay in departure at the end of the season, up to a point where departure was not delayed any further (Fig. 12). There was no link between the date of egg laying and the onset of moult, but fattening prior to autumn migration started when moult had ended.

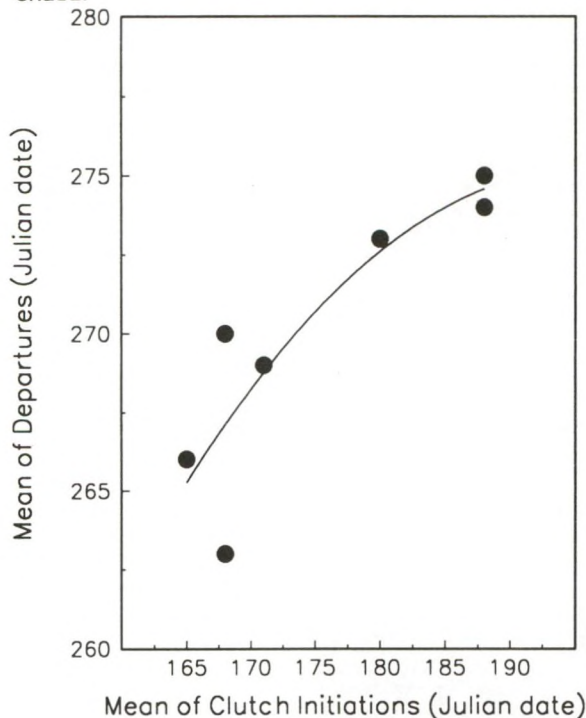


Fig. 12. Relationship of autumnal migration departure schedules of Mountain White-crowned Sparrows in relation to reproductive schedules. Seven years of data (Martin Morton).

MEASURING THE FITNESS CONSEQUENCES OF ARRIVAL DATE

Models that seek to calculate the optimal timing of the return journey to the breeding grounds must start from a relationship between fitness and arrival date and/or fitness and arrival condition (Fig. 9). Though the logic of the models requires adopting a life history approach, so far, students of migration have not attempted to actually measure the fitness consequences of alternative migratory decisions. This may well be due to the fact that "traditional" life history theory has concentrated on studying how decisions taken once a year affect mortality and reproduction (see reviews in LESSELLS 1991 and STEARNS 1992). State-dependent life-history theory (e.g. MCNAMARA & HOUSTON 1992) seeks to bridge the gap between behavioural ecology and life history theory. Still, fitness must be measured. In order to estimate fitness consequences of migration patterns we should know the relation between reproductive success, arrival date and nutrient stores upon arrival. In Fig. 9 the view is taken that optimal arrival date is independent of nutrient stores. However, the reproductive success as a function of arrival date is represented by the sum of the reproductive value of the offspring and the residual reproductive value of the parents. When the shape of the fitness curve over arrival time differs between offspring and parents, a trade-off over arrival time exists. When, in addition, the fitness of the parent but not the offspring (or vice versa) depends on the nutrient stores independently of arrival time, then the optimal arrival time will shift with nutrient stores. Fitness consequences of arrival date and condition cannot be estimated relying on natural variation between individuals. Just as in the study of clutch size (e.g. TINBERGEN & DAAN 1990), experiments aimed at manipulating arrival time to estimate fitness consequences for both parents and offspring are needed.

Even though the data are only observational, the review by DAAN *et al.* (1989) leaves little doubt that for single-brooded bird species the reproductive value of an egg declines in the course of the season. It is much less clear why this is so. There could be a link with competitive advantages related to the benefits of prior residence for either young competing on the wintering grounds, or adults competing on the breeding grounds, or both. When effects of prior residence are important, late-fledged chicks are at a clear competitive disadvantage during their first winter. Also, we would expect that early arriving breeding birds would be in the best position to take up the best territories (MYERS 1981). However, reviewing the evidence, KETTERSON & NOLAN (1983) suggest that "priority of arrival is not sufficient to establish an indefeasible claim when the claim is contested by a former owner". On the one hand there can be no doubt that local status is maintained from one year to the next in many

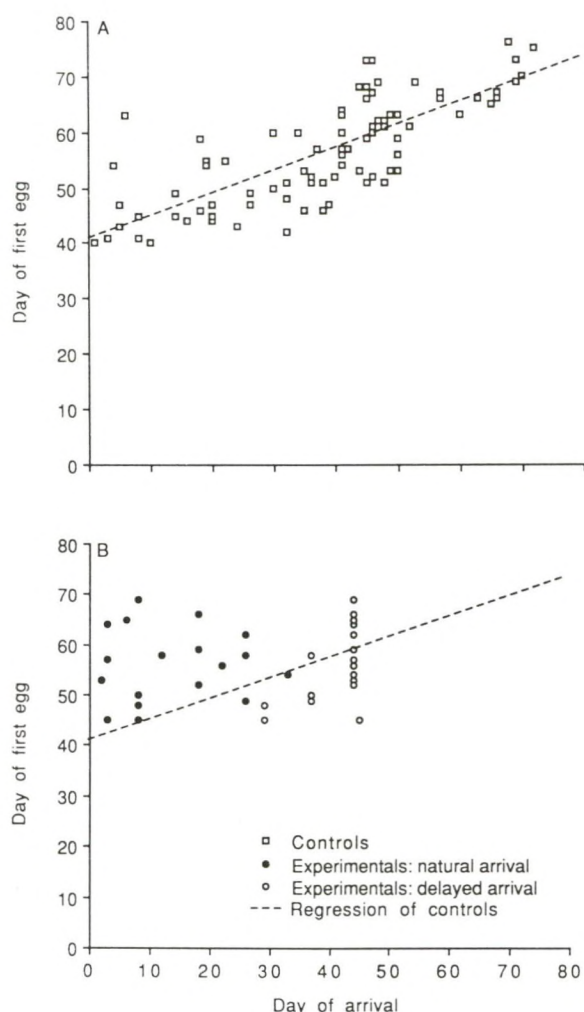


Fig. 13. Date of arrival and first egg (in days since first female arrived) for A) control and B) experimental females for 1990 and 1991 combined. Regression equation (dashed line, $y = 40.7 + 0.41x$) was computed for controls only, and is also shown in B) for comparison. Open circles represent natural arrival and first egg date for experimental females. Solid circles represent the dates of release from captivity and first egg for the same experimental females. (CRISTOL MS)

migratory long-lived species like the Oystercatcher. On the other hand it would seem that preempting potential usurpers by arriving early on the breeding grounds is less costly than evicting established usurpers (ignoring the cost of departing early from the wintering grounds). The longer Great Tits are experimentally removed from their territory the more likely it is that they will not succeed in regaining their territory (KREBS 1982).

Thus, methods should be found to measure the cost of arriving a certain number of days later than

potential competitors. The experiments of Dan Cristol (MS) go some way towards this goal. He showed that experimentally delayed female Red-winged Blackbirds (i.e. held in captivity for a while) were less often the first to breed in their harem and initiated clutches later, even though all females were released well before the first clutches were laid (Fig. 13). These negative effects on fitness, thought to result from a decline in social status, were much less severe when compared to the effects of a similar experiment on males (in a different population though), explaining why the polygynous male Red-winged Blackbirds tend to arrive earlier and much more synchronized than the females.

WHICH MODELS ARE BEST?

Fig. 9 depicts the timing of arrival as a simple optimization problem. However, the above discussion strongly suggests that the concepts of game theory (MAYNARD SMITH 1982) need to be applied, since what matters is not so much the absolute date of arrival, but the relative timing with respect to the arrival of potential competitors. This poses further problems for fitness measurements as well as for model builders. At this stage we must ask ourselves how to proceed as there seems a clear danger that the enterprise will lead to a forbidding graveyard of abandoned and undeveloped models none of which are rigorously tested. We suggest that the theoreticians should see it as their task to make clear under what conditions the more complex, but supposedly more realistic, dynamic optimization models yield the same predictions as the more elegant and analytically tractable rate-maximization models. The empiricists on the other hand should only abandon models if they consistently fail empirical tests. The model of ALERSTAM & LINDSTRÖM (1990) has inspired some good tests (LINDSTRÖM & ALERSTAM 1992) and should inspire more.

THE FULL ANNUAL CYCLE AS AN INDIVIDUAL DECISION

Noël Holmgren and Anders Hedenström were the only ones brave enough to tackle the full annual cycle in their application of dynamic programming to define the conditions when moult should take place. Pilfering from the abstract of the paper by Noël and Anders on this topic (chapter 3 in HOLMGREN 1993): "The scheduling of moult was basically a result of a trade-off between having a high feather quality during breeding versus during the non-breeding period. When feather quality was of major importance for survival, summer moult tended to be the optimal policy. In the opposite situation, when feather quality was more important during breeding, winter moult tended to be optimal. A

high impact of feather quality on survival rate in combination with low costs of moult resulted in biannual moult (summer and winter moult). Winter moult became more likely as the survival rate *per se* increased. Moult duration, migration costs and reproductive success *per se* were found to have no impact on the timing of moult." Though the assumption that feather quality affects fitness seems quite reasonable, the participants of the workshop knew of little direct evidence, let alone estimates of the magnitude of the effect. Since then, the work of Dale Clayton and coworkers on feather lice, heat loss and mate choice (BOOTH *et al.* 1993) was brought to our attention by Ellen Ketterson.

POPULATION DYNAMICS OF MIGRATORY SPECIES

So far we have considered a migration schedule as a sequence of individual decisions. What we have to compare our models with though, is the migratory behaviour of a population of individuals. This suggests that a complete understanding requires that we are also able to predict the number of birds that follow a particular migration strategy. This, in turn, forces us to ask how migratory birds affect each other. We already touched upon this question when investigating the effect of arrival time on fitness.

Though there are many ways in which the migratory decisions of one individual may be affected by the decisions of other individuals (due to the benefits of flying in a flock for instance; see discussion in PIERSSMA *et al.* 1990) the workshop concentrated on the effects of intraspecific competition on the breeding and wintering grounds. In his book "Populations in a seasonal environment" FRETWELL (1972) graphically investigated the consequences of density-dependent reproduction on the breeding grounds, and density-dependent survival on the wintering grounds. Here, density-dependent means that, with increasing population density, reproduction in summer or survival in winter are negatively affected. He showed that, depending on the shape of the relationships, regulation of the population occurred primarily in winter, during summer or in both seasons (Fig. 14). GOSS-CUSTARD (1980) developed an essentially similar simulation model. Remarkably, it is only now that these models are being followed up by attempts to obtain empirical estimates of the parameters and more penetrating theoretical investigations, like inclusion of the cost of migration, and attempts to derive the population model from knowledge of the behaviour of individuals.

John Goss-Custard presented the results of a collaborative effort to amass all available data on breeding and survival of the European populations of the Oystercatcher (GOSS-CUSTARD *et al.* in press (a); GOSS-CUSTARD *et al.* in press (b)). Assuming strong

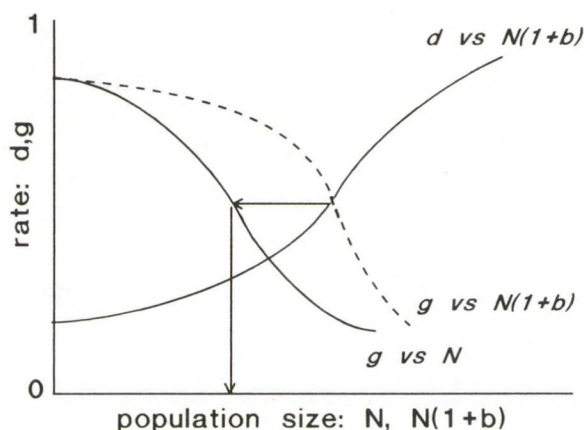


Fig. 14. Graph of a very simple model of population regulation in a seasonal environment. Production occurs during the breeding season with rate b , while deaths are confined to winter and occur with rate d . The population is stable if $d=b/(1+b)$, i.e. if the death rate equals the "replacement rate" g . The equilibrium autumn population size $N(1+b)_{eq}$ is found by plotting both g and d against the autumn population size $N(1+b)$. From FRETWELL (1972).

density dependence in summer, it was calculated that populations would decline following habitat loss on the wintering grounds, if wintering densities exceeded those where winter mortality became density-dependent. With steeper density dependence more birds would be lost. Though the database is impressive, the most important parameters, i.e. those describing important aspects of the density-dependent relationships, are least well known. To derive these population parameters from knowledge of the behaviour of individuals (see GOSS-CUSTARD & DURELL 1990) a game theory model of how Oystercatchers distribute themselves over the musselbeds in the Exe estuary was constructed. From this, a relationship between winter mortality and population size could be derived. The conceptual framework of the model presented by Paul Dolman was essentially similar, but its implementation differed. Instead of splitting the problem into several submodels, each with empirically estimated parameters, Paul Dolman presented a general simulation model incorporating all the processes believed to be relevant (Fig. 15, SUTHERLAND & DOLMAN in press). Below, the pros and cons of these conceptually similar models are investigated through a close examination of the components, confronting the assumptions with the relevant insights of other participants to the workshop.

DENSITY-DEPENDENT REPRODUCTION

Density-dependent reproduction will occur when with increasing population size an increasing proportion of birds settle in habitat of poor quality or do not breed,

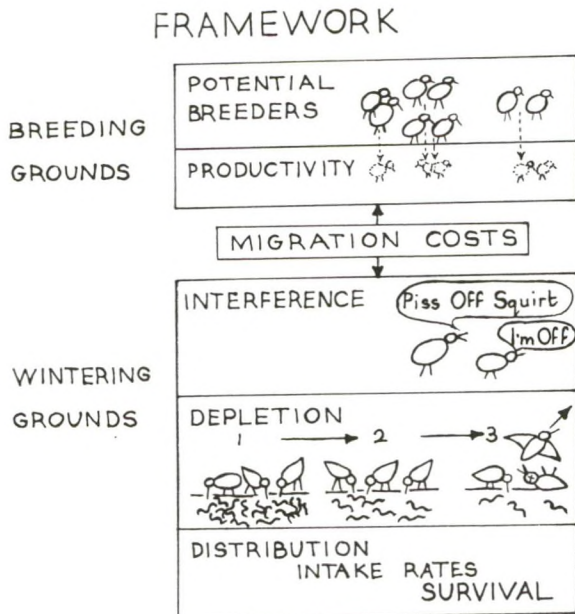


Fig. 15. Diagram depicting the presumed nature of the density-dependent processes on the breeding and wintering grounds (Paul Dolman).

the so-called buffer effect (KLUIJVER & TINBERGEN 1953). Detailed long-term studies of the American Redstart and the Blackthroated Blue Warbler by Richard Holmes and colleagues provided evidence for variation in habitat quality affecting fitness, leading to competition for high quality habitats, where food is abundant and nest predation low (HOLMES *et al.* 1992; SHERRY & HOLMES 1992). In Oystercatchers, intense competition exists for territories of high quality, where transport costs of food to the chicks are low (ENS *et al.* 1992). ENS *et al.* (MS2) suggest that potential recruits face a trade-off between immediately settling in a territory of poor quality or queuing for a territory of high quality. Thus, the only freedom left to the newly arriving nonbreeders when faced with intense competition is the decision on how to cut their losses: losing fitness in time (by queuing for a high quality territory) or losing fitness in space (by settling in a poor quality territory). Queuing must result from the advantage enjoyed by prior residents in the competition for space and the impossibility of maintaining high status over a large area (ENS *et al.* MS1). Despite the evidence for competition (see also the section on the fitness consequences of arrival date), the shape of the curve relating reproduction to the number of potential settlers remains elusive. Whereas differences between individuals are thought to be of critical importance in models describing density-dependent winter survival, such individual differences were not explicitly incorporated in the submodels of John Goss-Custard and Paul Dolman dealing with density-dependent reproduction. There

is a clear need to derive the density-dependent relationships from the accumulating knowledge on the mechanism of social competition during the breeding season.

DENSITY-DEPENDENT WINTER SURVIVAL

Winter survival will be density-dependent when food stocks can be depleted, or when interference forces an increasing number of birds into habitats of poor quality with increasing population size. Evidence for massive depletion of food stocks by various species of waterfowl on migration was provided by Mennobart van Eerden. In some examples food was depleted to a same threshold level each year, before the birds moved on, while in other examples the threshold level was variable (VAN EERDEN 1984; DRENT & PRINS 1987). The latter may have been due to variability in the food supply at preceding staging sites, and/or the need to arrive on the wintering site at a certain date. In contrast, wintering Oystercatchers rarely remove more than 30% of the standing stock over the winter, but interference is a well-established phenomenon, including the observation that individuals differing in dominance suffer to a different degree from the presence of conspecifics (ENS & GOSS-CUSTARD 1984; GOSS-CUSTARD *et al.* 1984). Subsequent theories on the distribution of unequal competitors have coined the term "competitive ability" to describe these differences between individuals (SUTHERLAND & PARKER 1985; PARKER & SUTHERLAND 1986). However, this concept may not apply in the field (see appendix I). For instance, it is hard to identify the better competitor with respect to the acquisition of food when there is a trade-off between foraging ability and fighting ability. Good foragers may have higher survival chances when food supplies are severely depleted, while good fighters can exclude other birds from the best feeding areas. Potentially, such a trade-off might explain why SHERRY & HOLMES (MS) did not find significant survivorship differences between American Redstarts wintering in different habitats, even though removal experiments showed that males despotically excluded females from certain habitats (MARRA *et al.* 1993). Furthermore, social dominance is not necessarily solely determined by relative fighting ability, but may also be determined by prior residence, especially when individuals show a strong site fidelity. Present evidence certainly allows the suggestion that Oystercatchers wintering on musselbeds "queue" for positions of high local dominance (ENS & CAYFORD, *in press*). The experiments of Dan Cristol on Dark-eyed Juncos left little doubt that behavioural dominance is influenced by situational factors, like arrival date (prior residence increases dominance, CRISTOL *et al.* 1990), hunger (lean birds are initially dominant, CRISTOL 1992) and the familiarity with a more dominant bird, as well as attributes of the birds like sex. Detailed studies of the White-throated Sparrows

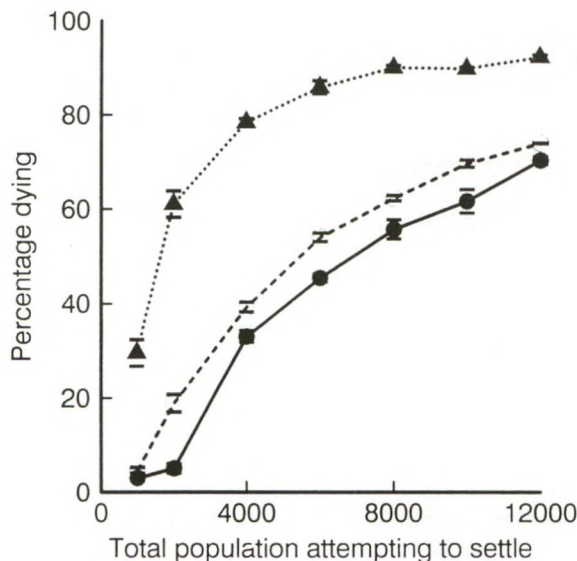


Fig. 16. The proportion of Oystercatchers predicted to die on the Exe estuary in winter in relation to the total number arriving there in autumn (means of several model runs, bars represent one SE). The threshold intake rate values required for a bird to remain on the estuary were either 200 mg AFDM/5 min (open circles) or 150 mg AFDM/5 min (solid circles). The solid triangles show the effects of removing the best 30% of the total mussel area, assuming a threshold intake rate of 150 mg AFDM/5 min. From GOSS-CUSTARD *et al.* (in press (e)).

underline the importance of site-dependency as well as age and sex in determining dominance in the field (PIPER & WILEY 1989; PIPER & WILEY 1990; PIPER 1990).

The presented population models did not incorporate these details of the competitive process. John Goss-Custard derived the relationship between over-winter mortality and autumn population size from a game theory model of how Oystercatchers differing in their susceptibility to interference and in foraging efficiency distribute themselves over the musselbeds of the Exe (GOSS-CUSTARD *et al.* in press (c,d & e)). The model assumed that each individual would move to the musselbed where it would achieve the highest intake rate and that there were no costs to moving, in line with the essence of the assumptions of the ideal free distribution model (FRETWELL & LUCAS 1970) according to KACELNIK *et al.* (1992). Though the model will not be the last word on the subject (GOSS-CUSTARD *et al.* in press (e)) the exercise demonstrated beyond doubt that the precise shape of the density-dependent winter mortality can be derived from knowledge of the behaviour of individuals in combination with measurements of the distribution of resources (Fig. 16). In the model presented by Paul Dolman, density dependence in winter mortality not only resulted from interference, but also from prey

depletion. This made it necessary to assume that the ideal free distribution was reached at each time step. The conditions under which this assumption holds have been theoretically investigated by BERNSTEIN *et al.* (1988, 1991). Empirical evidence suggesting close tracking of fluctuations in habitat quality over a fairly wide geographical area was provided by Mennobart van Eerden through an impressive example on Teal. In some years one fifth of the European population concentrated in the nature reserve the Oostvaardersplassen, while in other years numbers were very low, in line with fluctuations of the food supply related to the management of the water levels (Fig. 17).

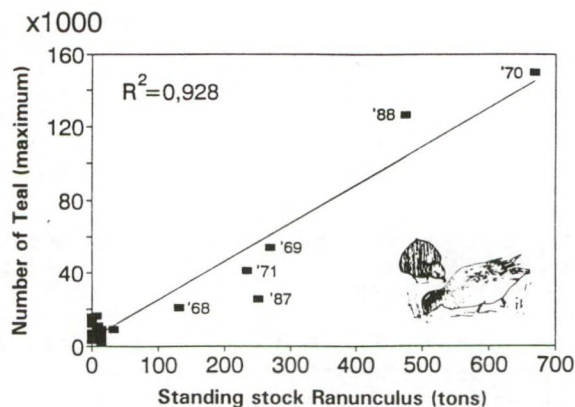


Fig. 17. The annual peak number of Teal in the freshwater marsh Oostvaardersplassen, Netherlands, plotted against the annual seed production of *Ranunculus sceleratus*. Large differences between years are due to manipulations of the water level. From VAN EERDEN & MUNSTERMAN (MS).

THE COST OF MIGRATION

Migration must be costly, but what are the costs and how high are they? For population models of migratory birds it is important to know if mortality on migration should be modelled as increasing only with distance, or as being density dependent as well. It has only recently become possible to estimate the contribution of the energy spent on migration to the annual energy budget (DRENT & PIERSMA 1990; PIERSMA *et al.* 1991; WIERSMA & PIERSMA, 1994). WIERSMA & PIERSMA (1994) have used heated taxidermic mounts to predict standard operative temperature, or, inversely, maintenance metabolism, for different microhabitats and weather conditions. This methodology allowed them to conclude that if *islandica* Knots, the subspecies that habitually winters on the intertidal mudflats of Western Europe, were to move to West Africa, habitually occupied by *canutus* Knots, they would incur a saving of 1.1 W on their maintenance metabolism and pay an extra 0.1-0.2 W to cover the cost of travel (Fig. 18). The problem is

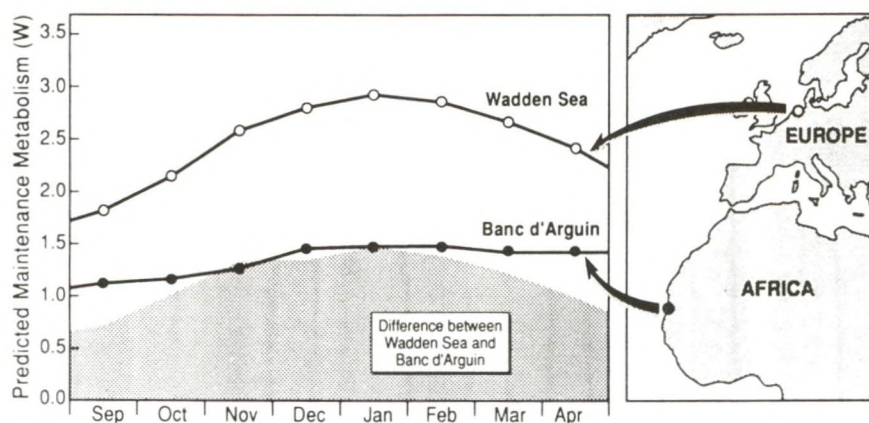


Fig. 18. Maintenance metabolism on the temperate Dutch Wadden Sea and on the tropical Banc d'Arguin, Mauritania, West Africa predicted for *islandica* Knots on the basis of meteorological data and microhabitat specific equations. These equations were calibrated with the use of heated taxidermic mounts. From WIERMSA & PIERSMA (1994).

that it is not clear how energy expenditure relates to survival and prospects for reproduction.

To calculate how birds from different breeding grounds should distribute themselves over wintering grounds at different distances, Paul Dolman simply assumed the existence of a critical intake rate, necessary to achieve the breeding grounds. The critical intake rate was thought to increase linearly with distance between the wintering and breeding grounds. Instead of assuming that birds with low intake rates do not reach the breeding grounds at all, it seems more likely that they will reach the breeding grounds later, probably at the cost of a reduction in reproductive success (Fig. 9). Both assumptions lead to density-dependence in either mortality or reproduction following migration for which there exists no empirical evidence whatsoever. An alternative assumption could therefore be that the crossing of a certain distance carries a fixed mortality risk. Estimating this risk is difficult. Peter Evans concluded that for several species of waders the actual mortality during the migratory journey is low relative to the mortality on the wintering and the breeding grounds (PIENKOWSKI & EVANS 1985; EVANS 1991). The reverse seems to be the case for the small migratory passerines studied by Dick Holmes and colleagues (HOLMES *et al.* 1989; HOLMES & SHERRY 1992). Martin Morton reported that there existed no differences in age-specific survivorship curves between a migrant and a nonmigrant subspecies of the White-Crowned Sparrow. A problem with all these survival estimates is that it is not possible to separate lack of fidelity to the wintering or breeding area from mortality. The only conclusive solution to this problem is to study a significant part of the population throughout the year, as can be done in some species of geese (e.g. OWEN &

BLACK 1989; EBBINGE *et al.* 1991). This will also help in testing the suggestion of PIENKOWSKI & EVANS (1985) that an important reason for minimizing the flight distances on the first migration is to reduce the risk of failing to complete the journey to a suitable "wintering" site, i.e. adults may not suffer high losses on migration, but the inexperienced juveniles may.

PREDICTING THE EFFECTS OF HABITAT CHANGE

An important incentive in several of the previously discussed studies was the desire to understand and, if possible, predict the effect of man-induced habitat changes on the population dynamics of the migratory birds. Such man-induced changes range from local reclamation of some of the mudflats in an estuary to global climate change. A unifying theme in the studies of Dick Holmes and co-workers for instance has been the desire to identify the causes of the dramatic decline in the numbers of neotropical migrant passerines (HOLMES & SHERRY 1992; SHERRY & HOLMES 1992; SHERRY & HOLMES *in press*). GOSS-CUSTARD *et al.* *in press* (a) used their population model to calculate the effect of loss of wintering habitat on the equilibrium population size of the European population of Oystercatchers (GOSS-CUSTARD *et al.* *in press* (b)). They arrived at the startling conclusion that the coastal subpopulations would be strongly negatively affected by habitat loss, while negative effects on the inland breeding subpopulations only became apparent after the coastal subpopulations were decimated. There is a clear need to test the underlying assumption that coastal and inland birds compete on equal terms on the wintering grounds.

When the ESS migration model of SUTHERLAND & DOLMAN (in press) was used to predict the effect of habitat change on the numbers of birds using different migration routes, it was assumed that the birds can adapt to the new circumstances, culturally or genetically, i.e. a new ESS can be achieved. BERTHOLD & QUERNER (1981) and BERTHOLD (1988) have shown the existence of genetic variation in the migratory behaviour of the Blackcap. BERTHOLD *et al.* (1992) provide evidence that this species has evolved a new migration route over the past 30 years. Instead of assuming that a new ESS is reached in response to habitat loss without problems, Paul Dolman (unpublished) therefore theoretically investigated the conditions under which a species with a genetically determined migration strategy could survive a drastic change of habitat. The model showed that for the migration strategy to track the changing environment, it was important to have sufficient genetic variance in the population. The model also showed that assortative mating can allow a much more rapid response, allowing tracking even when the level of genetic variation is initially very low.

CONCLUSIONS

SOME IMPORTANT AND HOPEFULLY AMENABLE PROBLEMS

While discussing the various migratory decisions in turn, a host of problems was encountered. It seems prudent to make a short list of the most important ones.

- Though energy is rightly described as the fire of life (KLEIBER 1961), an animal must also retain water and protein balance during the migratory flight, topics that deserve and attract increasing attention.
- There can be little doubt that the power curve is central to predictions on speed, altitude and range of the migratory flight, itself a crucial element of any migration schedule. Though there was general agreement that the power curve must be U-shaped, it was felt that much more empirical work was needed to confirm the precise shape for a given species, a necessary prerequisite for reliable quantitative predictions. On the basis of empirical evidence it is impossible to decide between the models of PENNYCUICK (1989) or RAYNER (1988), but the former has fewer and more easily measured parameters than the latter.
- Migration must be costly, but what are the costs and how high are they? It is intuitively appealing to assume that high energy expenditure reduces survival (e.g. DAAN *et al.* 1990), but nothing conclusive is known. For population models of migratory birds it is important to know if mortality on migration should be modelled as fixed for a given distance, or as density dependent.

- Though there is an increasing awareness that population models should be derived from the interactions between individuals, the models discussed contained assumptions about the competitive process that may be untenable. One of the authors of this report feels rather strongly that empirical studies of the competitive process would benefit from a clarification of concepts (see appendix I).

MIGRATORY BIRDS PROVIDE GOOD RESEARCH SYSTEMS

In the above we have listed what were considered to be the most important problems, written from the perspective of a scientist who has decided, for whatever reason, that solving the mystery of bird migration is what he wants to do with his life. However, scientists wanting to solve a different problem should in no way feel excluded. If the study of migration strategies is to become a serious undertaking direct fitness measurements must be taken. Thus, there is a clear need for a closer link between migration and breeding biological studies of the same populations. In fact, it is even possible that scientists with different interests will find that migratory birds are particularly suitable for answering their questions. The following suggestions came forward:

- Birds preparing for migration may offer good opportunities for studying whether foraging behaviour is risk prone or risk averse. The problem seems that field workers lack a search image for such behaviour: the theoreticians should come forward with suggestions of what to look for.
- Migratory birds may offer better opportunities for studying seasonal timing of moult and reproduction than sedentary birds. Attention should focus on arrival time and the experimental manipulation of that arrival time.

PROSPECTS

The workshop left the participants with little doubt that the study of bird migration, in particular the study of migration schedules, is rapidly gaining momentum through the application of the same ideas and techniques, first developed by economists, so successfully applied in other fields of behavioural ecology. To maintain momentum it is necessary that the more empirically minded and the more theoretically minded students of migration continue to remain in close contact. To minimize the damage of excessive social competition it is necessary that this contact is not only established through the scientific literature, but above all through personal contacts. A close cooperation between theorists and empiricists would fit the tradition of behavioural ecology. It will be important though to avoid repeating a common mistake of many behavioural ecologists, who have neglected the study of mechanism at the expense of the study of the evolutionary costs and benefits (HUNTINGFORD 1993).

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APPENDIX I: COMPETITIVE CONCEPTS

During the workshop and the following gestation of this report it became clear that my dislike of some terms and concepts was not shared by the majority of participants. Since muddled concepts will lead to muddled investigations, I felt inspired to write this appendix, where I try to make clear on what basis I distinguish between useful and confusing concepts. A concept is considered useful when it has a clear definition and, in principal, allows taking measurements. A concept is considered confusing when it has been used in many different ways, even though it was originally clearly defined. A concept is also considered confusing if it has no clear meaning when applied to a real world situation, even though it may be precisely defined in a mathematical model attempting to describe that real world situation.

USEFUL CONCEPTS

social dominance

Aggregate measure of success in winning encounters at a given location against a specified set of opponents, probably depending on both relative fighting abilities and payoffs of focal animal and opponents. It is often wrongly thought of, not as a relationship, but as the ability of an individual to dominate others. This is due to the habit of calculating dominance scores without making reference to the opponents or to the location (e.g. ENS & GOSS-CUSTARD 1984).

fighting ability

The ability of an individual to win fights when payoffs and positional advantages are controlled for. It should not be confused with social dominance, which refers to a relationship and not a true ability of an individual. Though the concept is easy to grasp, it is rather evasive when it comes to actual measurement. This is because it is very hard to control for all the confounding factors.

payoff to winning a contest

Increase or reduction in the reproductive potential of an individual when it either wins or loses a contest; it should be measured as the change in Expected Future Reproductive Success (EFRS); see GRAFEN (1987). Though quickly understood on paper, it is very hard to actually measure. Measurement inevitably involves many additional assumptions.

foraging ability

The ability of an individual to find food. It can be derived from what GOSS-CUSTARD & DURELL (1988) have called the Interference Free Intake Rate (IFIR) by controlling for prey density. IFIR is measured as the rate of food intake that an individual achieves in a certain location when it is not hindered by other individuals. There could well be a trade-off between foraging ability and fighting ability, since designing an animal that is good at fighting may conflict with demands that make the animal good at exploiting resources. In fiddler crabs females have two small claws for picking up food, while in males one of these feeding claws is enlarged to such an extent that it can no longer be used for feeding, but it is very effective in fighting with conspecifics, as well as in attracting females (CHRISTY & SALMON 1984). It is my hunch that in many species, males may be better at fighting over resources and less efficient at exploiting these resources at low resource levels compared to females.

susceptibility to interference (STI)

The rate at which food intake declines when the number of competitors increases, most often measured as the slope of the relationship between intake rate and competitor density (GOSS-CUSTARD & DURELL 1988). Ideally, it should be controlled for prey density, but to my knowledge this has never been done.

CONCEPTS CAUSING CONFUSION

resource holding potential (RHP)

When PARKER (1974) launched his theory that the outcome of encounters will depend on both the fighting abilities (e.g. weaponry or physical strength) and the payoffs to the individuals involved, he used the word Resource Holding Potential (RHP) instead of fighting ability. Though intended as a clarification, the term RHP has given rise to much misunderstandings in my opinion and should, perhaps, be dropped. As far as I understand it, the reason for adopting the term RHP is that it also includes positional advantages. Two knights might benefit equally from gaining access to a princess and might be equally good fighters, but if one has to fight uphill the odds are against him. Similarly, a male toad may ward off rival males more easily when it is in amplexus with the female than when he swims near to her. Thus, when using the word fighting ability instead of resource holding potential, it is important to keep in mind that there could be positional advantages, which should be unrelated to the payoffs though.

competitive ability

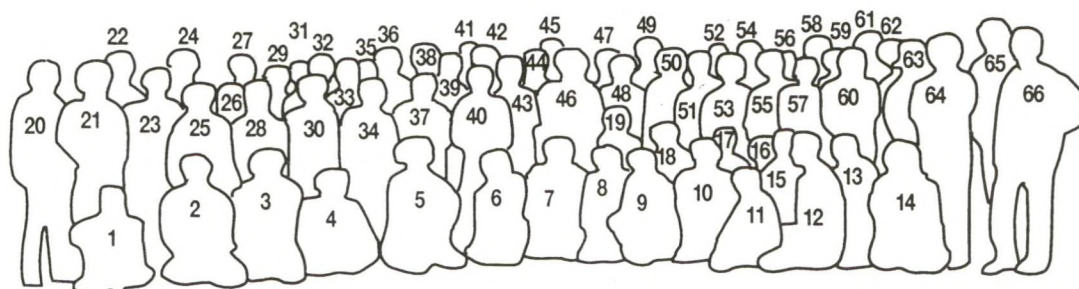
My principal problem with the concept of competitive ability is that it creates the impression that it can be measured as a single character of an individual. I think that to be highly unlikely. As used by SUTHERLAND & PARKER (1985), competitive ability indicates the ability to acquire resources when competing with other individuals and it is more or less equated to susceptibility to interference, i.e. the rate at which food intake declines when the number of competitors increases. Susceptibility to interference depends on local dominance and it is very likely that local dominance depends on both payoffs and fighting ability. Whereas fighting ability is a true ability of an individual, social dominance is not. We might decide to equate competitive ability to fighting ability, but I think little would be gained from two terms for a single concept. Furthermore, the point about competitive ability is that it describes the success in competing for resources. When scramble competition is the most important process, foraging ability, instead of fighting ability, is what matters. When both contest and scramble competition matter, we need to measure both foraging ability and fighting ability and the possible tradeoff between these two abilities would destroy any hope of measuring competitive ability as a single character. In fact, a tradeoff seems inevitable to me, since the attributes that make an animal good at fighting are different from the attributes that make an animal good at foraging.

(written by Bruno Ens)

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