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Life History of the Common Gull (*Larus canus*)

A Long-Term Individual-Based Study

KALEV RATTISTE

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Abstract

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An individual's life history is a sequence of events which eventually determine its contribution to the next generation, or fitness. These events are affected by environmental factors, genetic make-up and decisions made by an individual and its breeding partner. Recognition of these determinants helps to understand both short-term ecological changes and long-term evolutionary dynamics in a population. In this thesis long-term individual-based data on common gull (*Larus canus*) is used to study age-dependent reproductive success, survival, pair retention and breeding time. Collected pedigree data enabled to study genetic variation of traits and the selection on them.

The reproductive success of common gulls increased steadily until very old age. This increase cannot be explained by selection effects, since individuals with lower breeding success were shown not to have lower survival. Consequently, this gain must be ascribed primarily to an age-related improvements of individual competence and/or increased reproductive effort. Annual survival of adult birds was age- and year-dependent. The latter was partly explained by winter severity. The size of the white spots on five outermost primaries predicted the bird's future survival and divorce probabilities and hence, pair endurance capability. Gulls with larger spots enjoyed higher survival and lower divorce rates compared to birds with smaller spots. This suggests that the wing tip pattern might function as a condition dependent signal, revealing individual variation in quality. One of the advantages of persistent pair bond was the ability to start breeding early in the season. The timing of breeding of firm pairs advanced with time not only due to mates' increasing age, but also owing to their experience together. Although both sexes had phenotypic effects on laying date, it was heritable only in females. On the phenotypic and genotypic level, early laying was under positive fecundity and survival selection in females.

Keywords: Larus canus, longitudinal studies, reproductive success, survival, pair bond, indicator trait, breeding time, heritability, selection

Kalev Rattiste, Department of Ecology and Evolution, Department of Animal Ecology, Norbyv 18 D, Uppsala University, SE-75236 Uppsala, Sweden

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To Sven Onno, my parents and family

Common gulls – drawing on the cover by Triin Tiits

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

I Rattiste, K. (2004) Reproductive success in presenescent common gulls (*Larus canus*): the importance of the last year of life. *Proceedings of the Royal Society of London Series B Biological Sciences* 271: 2059–2064.

II Rattiste, K. & Lilleleht, V. (1995) Survival rates of breeding common gulls in Estonia. *Journal of Applied Statistics* 22: 1057–1062.

III Rattiste, K. & Saks, L. Wing tip pattern predicts future survival and divorce probability in common gulls (*Larus canus*) (Manuscript).

IV Brommer, J.E. & Rattiste, K. Selection on the seasonal timing of reproduction in the common gull *Larus canus*: Roles of the sexes, of genes, and of the environment (Manuscript).

V Larsson, K., Rattiste, K. & Lilleleht, V. (1997) Heritability of head size in the common gull *Larus canus* in relation to environmental conditions during offspring growth. *Heredity* 79: 201–207.

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Contributions

The order of the authors reflects their involvment in the papers. I have personally written, and performed all analyses in papers I, II and III. Coauthors discussed ideas and commented on the text. For papers IV and V analyses and writing were made primarily by the first authors and partly by me. V. Lilleleht and L. Saks have contributed to data collection. The long-term study was initiated in 1962, I joined the project in 1972.

Contents

Introduction

Long-term individual-based studies are essential for understanding both short-term ecological changes and long-term evolutionary dynamics in a population. Such studies allow following each individual during its lifespan, and thus provide an understanding of individual life history (the schedule of reproduction and survival over age classes) from a longitudinal perspective. Furthermore, only through continuous study can information on relatives be gathered. Such information is needed to calculate the genetic variation in traits and the selection on them; both these are needed to understand evolutionary changes. The majority of individual-based studies in the wild consider relatively short-lived species, but there are good reasons to suspect that findings based on short-lived species are not extended easily to long-lived ones. For example, the influence of individual experience and of the stability of the pair bond on reproductive output are mainly important aspects in long-lived species. This study considers a long-term study of common gulls *Larus canus*, many which are individually marked right after hatching and subsequently followed throughout their lives. Using this information, I study the following questions in this thesis:

- How does an individual's reproductive success change during its life?
- Is survival affected by an individual's intrinsic quality?
- Which environmental factors affect annual survival?
- Does individual's current condition affect breeding pair stability?
- Which are the advantages of persistent pair-bond?
- Which indicator traits can be used by a bird to evaluate potential mates?
- Is laying time heritable and under selection? If yes, then does selection act both on genotypic and environmental component of this trait?
- Are heritability estimates obtained under different environmental conditions affected by genotype x environment interactions?

The relationship between individual experience/age and reproductive success in birds is well documented (reviews in Ryder 1981, Clutton-Brock 1988, Saether 1990). Generally, reproductive performance increases with age during the first reproductive years, stabilizes at middle age and sometimes declines in old age as an expression of senescence. A multitude of explanations have been proposed for the increase of mean reproductive success in young individuals. Forslund & Pärt (1995) classified these explanations in three major groups: (i) progressive appearance or disappearance of phenotypes (the selection and delayed breeding hypotheses); (ii) age-related improvements of competence (the breeding experience and constraint hypotheses); (iii) optimization of reproductive effort (the restraint hypothesis). These hypotheses are not mutually exclusive and may act in concert to create an increase in reproductive performance with age (Wooller *et al.* 1990; Forslund & Pärt 1995).

Although several studies have shown differential survival for good and poor performers (e.g. Coulson & Porter 1985; Nol & Smith 1987; McCleery & Perrins 1988; Birkhead & Goodburn 1989; Wooller *et al.* 1990; Smith 1993; Laaksonen *et al.* 2002), the selection hypothesis is not supported in most species examined (Forslund & Pärt 1995; Martin 1995). However, the applied tests may suffer from a methodological problem (I). In particular, these tests necessarily rely on estimates of breeding success in the terminal breeding occasion for non-survivors. In contrast, the focal breeding occasion is not the ultimate one for survivors. If the breeding performance of last time breeders is reduced compared to previous breeding events, there is a risk of systematic error, since performance in the ultimate year of life may not reflect an individual's overall quality. To overcome this problem, the assessment of the selection hypothesis should not involve ultimate breeders, which would allow an unbiased test of whether individuals of inferior general quality (i.e. poor performers) indeed have a lower probability of survival than birds of higher quality (I).

In addition to individual properties such as experience, also reproductive output may be affected by quality differences across years (I). Such environmental effects may also affect the survival of individuals (II). Understanding the nature of such annual effects will be ecologically important. Nevertheless, in order to gain a proper estimate of survival from individual-based data, potential differences in capture probabilities across sexes and years need to be controlled for. By using of statistical models that implicitly incorporate the capture-recapture nature of individual-based data, accurate descriptions of survival probabilities can be obtained, and related to climatic conditions (II).

Reproductive success will not only depend on an individual own experience in breeding (I), but may also depend on its partner's quality (III).

In sexual organisms each individual faces the basic problem of having to form mating relationships in a way that maximizes its fitness. High reproductive success means not only to produce as many offsprings as feasible, but also to produce offspring of as high quality as possible. Pair endurance ability is of special importance in long-lived monogamous species such as the common gull, because breakage of an established pair bond may result in significant fitness costs. There are two causes of pair bond breakage, the death of a partner and divorce. Hence, long-lived birds should try to avoid pair bond breakage by making a proper mate choice. However, choosers oppose the considerable problem of assessing their potential mate's quality and must therefore rely on some correlated trait, or ornament. Still, the evolution of these sexually selected traits is poorly understood and disputed, especially in relation to pair bond stability. In general, ornaments are thought to serve as indicators revealing the phenotypic and possibly also the genetic quality of their bearer. The honesty of the signal would be ensured by its high cost, so the individuals of inferior quality could not afford to cheat (Zahavi 1975; Grafen 1990; Iwasa *et al*. 1991). Most studies consider the role of male ornaments within the context of a polygynous mating system.

Although numerous studies have demonstrated correlations between ornament expression and individual quality, the data on the connections between ornaments and future survival in long-lived monogamous species has remained scarce and equivocal (Andersson 1994; Jennions *et al*. 2001; Jones *et al*. 2004). Further, several hypotheses about the divorce in birds (Choudhury 1995 and Black 1996) suggest that the ultimate cause of divorce is a relatively poor breeding success (Dubois & Cézilly 2002) or the prospect to improve it. Obviously, breeding success directly or indirectly reflects the quality of the breeding partner and one may thus expect a negative relationship between ornament expression and divorce rate. So far, only one study has investigated this relationship. Jones & Montgomerie (1991) found that in least auklets (*Aethia pusilla*) males with larger facial plumes were more likely to reunite with their mate the next year than males with smaller plumes.

The advantages for persistent pair bond in longed-lived birds species consist of both avoiding costs of pair breakage, and of gaining pair retention benefits. The main cost for a widowed or divorced mate is the time and energy to be spent on searching for a new mate (Real 1990). Thus, pair breakage costs can be easily characterised by a delay in breeding time. The description of costs and benefits in terms of breeding time is especially appropriate since laying time is known to be under strong positive fecundity selection in many bird species (e.g. Sheldon *et al*. 2003). However, the evaluation of pair retention benefits in terms of breeding time is not straightforward due to the confounding effect of advanced breeding with increasing age. Therefore, longitudinal analysis of annual laying time among groups with different pair duration is needed. Further, if ornament expression is correlated with survival and divorce (i.e. pair duration capability), and persistent breeding pairs start to breed earlier, then the relationship between ornament expression and laying time would be expected as well.

The wing tip patterns of several gull species have been shown to be highly variable, age dependent and sometimes also sexually dimorphic (e.g. Coulson *et al*. 1982; Allaine & Lebreton 1990). All these properties are characteristics to sexually selected traits (Andersson 1994). Similar white spots in otherwise pigmented plumage have been shown to function as sexually selected traits in other bird species (e.g. Höglund *et al*. 1990; Pärt &

Qvarnström 1997; Kose & Møller 1999). Moreover, as expected from reliable quality indicators, the white spots can inflict considerable cost upon their bearer. Melanized feathers are shown to be much more resistant to abrasion (e.g. Bonser 1995) and ectoparasites (e.g. Kose *et al.* 1999) than unmelanized ones. Thus, unmelanized feathers may be expected to be much more vulnerable to mechanical injuries than melanized ones which may lead to the reduction of feather area on the tips of the outermost primaries and significant reduction in flight ability (e.g. Møller 1991; Swaddle & Witter 1997). Hence, it is interesting to explore whether the size of the white spots on the tip of the wing may act as a condition-dependent signal in common gulls that can be used in a quality assessment of a potential mate (III).

Long-term studies are useful for studying individual effects (I ,II, III), but are also essential for studying evolutionary questions (IV, V). The offspring that recruit back into the breeding population provide one with an estimate of selection, and the resemblance between relatives can be used to estimate the genetical effects underlying trait variation.

Timing of reproduction within the season is an important fitness-related trait in many invertebrates and vertebrates. In birds, laying early in the season is known to give fitness benefits (e.g. Klomp 1970). Laying date also typically shows some heritability (e.g., van Noordwijk *et al.* 1981; Merilä & Sheldon 2000; van der Jeugd & McCleery 2002; Sheldon *et al.* 2003). However, no phenotypic change in laying date as a response to selection has been documented (reviewed in Merilä *et al.* 2001). These observations led Price *et al.* (1998) to develop a theory that could explain why a heritable trait like laying date, which is under selection, does not show an evolutionary response.

The Price *et al.* (1988) hypothesis hinges on separating genetic and environmental causes of trait variance and linking these components to selection (figure 1). In its simplest form, any trait T can be considered the sum of its genetic merit a_T and an environmental component e_T. For a single trait, the expected response to selection R is given by the breeder's equation, the product of trait heritability h^2 and the selection differential S describing the phenotypic covariance between trait T and fitness w (S = cov[w, T]). An evolutionary change is narrowly defined as a change in the breeding values in a population (Robertson 1966), and the breeder's equation $h^2 S$ is typically assumed to be an unbiased estimator of the selection differential on the breeding values S_a (= cov[w, a_T], figure 1A). However, Price *et al.* (1988) pointed out that a (non-heritable) environmental factor could affect both an individual's trait value and its fitness, which would lead to an environmental covariance between trait and fitness (cov[w, e_T]). For example, under good environmental conditions, individuals may breed early and enjoy high fitness because offspring survival is also high under good environmental conditions. As a result, the expected response based on the phenotypic selection differential will be greater than the selection differential on the breeding values (figure 1B), and will thus overestimate the potential response (Price *et al.* 1988). In the extreme case, most of the phenotypic selection can act on the trait's environmental component and not between the trait's genetic component and fitness (figure 1C), in which case no response to selection is expected even though a trait is heritable and under phenotypic selection (Price *et al.* 1988).

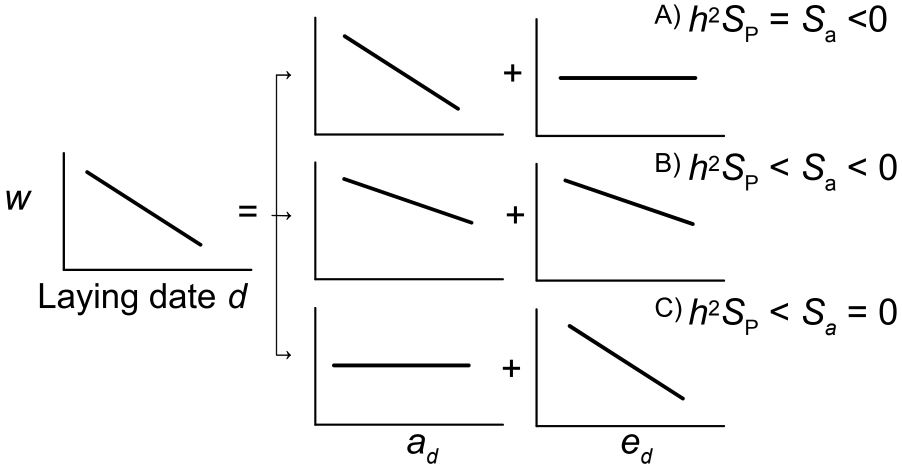

Figure 1. A schematic representation of three possible patterns of selection on the genotypic and phenotypic level leading to different outcomes when comparing the breeder's equation (h^2 S_P) with selection on the breeding values (S_a). The phenotypic selection on laying date S_P (the covariance between fitness and laying date *d*) is negative (left panel). (A) Selection occurs on the breeding value of laying date a_d, but not on the environmental component of e_d, which illustrates the assumption underlying the use of the breeder's equation. (B) As postulated by Price *et al.* (1988), selection may also occur on e_d thereby inflating the expected response h^2 S_P. (C) Selection occurs only on e_d, no evolutionary response is possible.

A significant selection on genotypic trait values refutes the idea that phenotypic selection is entirely due to environmental covariance (figure 1C), but does not exclude environmental covariance (it does not differentiate between the scenarios in figures 1A and 1B). Some studies have demonstrated a significant selection on the environmental deviations (e.g. Kruuk *et al.* 2002, Garant *et al.* 2004), which shows that the environmental component of a trait can be under selection. However, separate study of phenotypic and genotypic selection does not address the question if, and to what extent, the expected response is inflated. Studying this question requires a direct quantitative comparison of the expected response on the phenotypic versus the genetic level (Rausher 1992, Stinchcombe *et al.* 2002, Postma 2006, figure 1). To date, only one study has made such a comparison, and found no evidence of an environmental covariance between trait and fitness (Gienapp *et al.* in press), thereby not supporting the hypothesis of Price *et al.* (1988).

Knowledge about heritabilities and genetic correlations is necessary if one wants to make predictions about genetic responses to selection or reconstructions of evolutionary changes in the past (Lande, 1976, 1979; Lande & Arnold, 1983; Falconer, 1989). To be able to make accurate predictions about genetic responses to selection in heterogeneous natural environments, one needs to know not only the variability of selection pressures, but also whether heritability and genetic correlation estimates commonly vary over time and space (Arnold 1981; Via & Lande, 1985; Gebhardt-Henrich & van Noordwijk, 1991; Larsson, 1993; Merilä, 1996). It is also necessary to identify the mechanisms that may cause variation in the estimates of genetic parameters. Thus, to understand evolutionary dynamics, one needs also to understand variation in environmental quality since it may affect our estimates of phenotypic selection (IV) and heritability (V).

Study species and Population

The common gull (*Larus canus*) is a monogamous long-lived seabird breeding mainly in colonies. This species is appropriate for ecological studies since it has several advantages over other bird species. These advantages are:

- Breeding in colonies makes data gathering easy
- Both partners incubate and are catchable during incubation
- The sex of adult birds can be easily and reliably determined
- Adult birds can be marked with plastic rings, making their catching in following years unnecessary
- Chicks can be ringed in their first day of life
- Breeding birds are highly faithful to their nesting colony
- Natal fidelity of offspring is relatively high
- Birds are insensitive in relation to human activity in colonies

Common gull has a fixed clutch size of three eggs, and about 10% of all eggs produce recruits. Recruits start to breed at the age of 2-5 years, males at a younger age than females (on average at 3.2 and 3.7 years, respectively). Birds tend to breed with mates about of their own age. The pair bond persists on average for 2-3 years, but the most persistent pair recorded in our study population has bred together for 19 years. Annual survival is usually 89%. Common gulls breed on average for 5-6 years, but 20% of them breed for more than 10 years, and the oldest birds in the study area have bred for 26 years. Typically 50% of males and 10% of females return to breed in their natal colony and breeding individuals are faithful to the breeding site, less than 3% of them change their breeding colony between years. Hence, it is relatively straightforward to collect accurate individual-based data on common gull life history.

Common gulls started to colonize the islands of Matsalu Nature Reserve in the middle of 1950s. Their number increased rapidly until the middle of 1970s when pink-legged herring gulls started to expand eastwards from western Europe. Initially, herring gulls occupied marine islands far from the coast. Due to increasing predation by herring gulls, the breeding success of common gulls decreased heavily and eventually they deserted these colonies (figure 2). In spite of an overall reduction in population size in Matsalu Nature Reserve (figure 2), the number of breeding common gulls has steadily increased in our study area, which consists of three islands close to the coast.

The main reason for this population increase is that our main study colony has become the most favourite breeding site for common gulls in western Estonia, due to low number of herring gulls on this island.

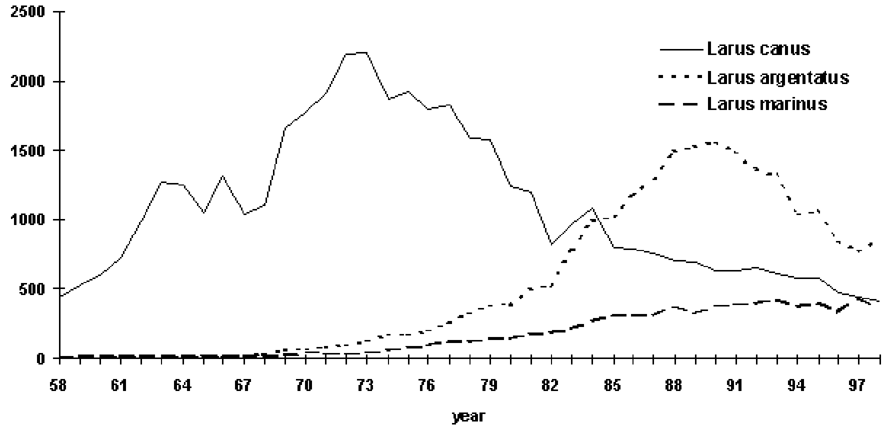

Figure 2. The number of breeding common (*Larus canus*), herring (*Larus argentatus*) and great black-backed gulls (*Larus marinus*) on islands of Matsalu Nature Reserve in 1958-1998.

Data collection

The long-term study of common gulls was initiated by Sven Onno in 1962. This research has continued until the present. The study area consists of three small islands (with an area of 0.5–3.7 ha) in Matsalu Nature Reserve, situated in western Estonia (58°46'N, 23°26'E). The number of breeding pairs has increased from 212 to 455 during the study period.

Long-term study needs reliable marking and recognition of individuals. Up to 1971, we marked adult birds with two aluminium rings to avoid possible bias of results from ring losses. From 1971 up to 1991 we used one aluminium ring and the individual combination of four celluloid rings (five different colours). Since 1991 we use engraved PVC rings with alphanumeric code. Every year, worn and missing plastic rings are replaced with new ones. Old metal rings are also replaced. Thus, the possible effect of ring losses on the results is negligible. Additionally, trapping and ringing of chicks and nesting adults on surrounding islands (within a radius of 2-3 km) is carried out regularly. Occasionally, this is also done farther away (within a radius of up to 65 km). As a result, the greater part of breeders in surrounding colonies are controlled and marked, as well. This allows us to detect immigration and emigration of adults to, and from the main study area.

By making everyday visits to the colonies, the date of laying and sequence of eggs, their weight and fate (predated, flooded, abandoned, a dead embryo, unfertilized, a chick hatched) are monitored. Nest owners are identified by observations from a mobile hide. First-time breeders are captured on nests with spring trap after the tenth day of incubation, sexed reliably according to the head length (if needed, controlled also by bird's behaviour) and ringed. As a result, at least 94% of adult gulls (both males and females) are identified every year. Almost all hatched chicks are ringed in their first day of life and chicks found dead later, are registered. At the end of the season all nests are mapped.

There are 2,300 complete (birds dead by now) and 900 incomplete (birds still alive) life histories of common gulls (reproductive life span, breeding years and partners, events of divorce and widowing, number of hatched, fledged and sexually mature offspring, lifetime reproductive success etc.).

Results and Discussion

Reproductive success (I)

In a cross-sectional analysis, the breeding success of common gulls increased with experience until the tenth breeding year and started to decline thereafter. In addition, equally experienced individuals had until their eighth breeding year lower breeding success in the ultimate breeding event than in the penultimate one, while in older birds this difference disappeared. As expected, in favourable years breeding success was higher than in unfavourable ones (figure 3).

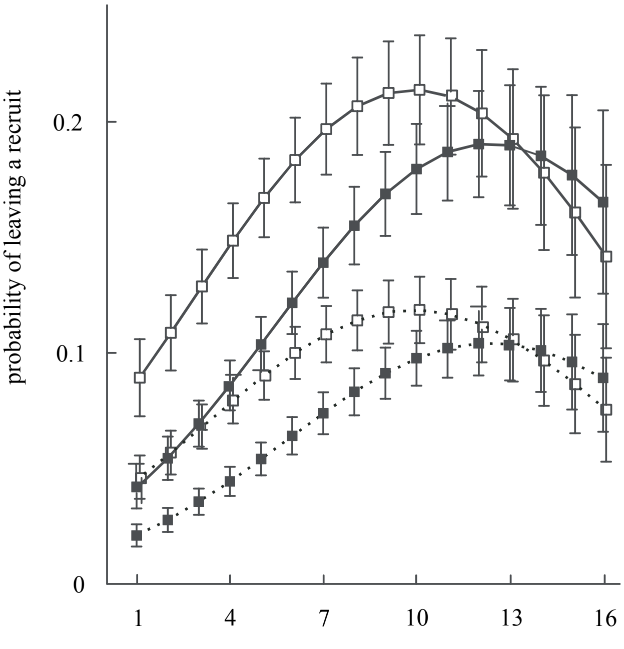

Figure 3. The breeding success of common gulls (predicted values from a model, see I) in relation to bird's experience, type of breeding year (solid lines, favourable; dotted lines, unfavourable) and breeding event (filled squares, ultimate year of life; open squares, penultimate year of life). Error bars represent ± 1 s.e., sexes pooled.

The breeding success of presenescent common gulls declines drastically before their death, suggesting a comparatively sudden decline in their condition. Thus, the low reproductive success in the terminal breeding event reflects a specific premortal decline in condition rather than individual's overall quality.

To test whether the increase in the average reproductive success with advancing age could be explained by selection effects, the survival of unsuccessful and successful breeders was compared both in the conventional and in an alternative way. The conventional approach compares the survival of poor and good performers to the next year. Here, the data set (set A, figure 4) involves three groups of breeders: (i) survivors in good condition (breeders a, b and c, figure 4); (ii) non-survivors in good condition during their ultimate breeding season (breeders d, figure 4); and (iii) non-survivors in poor condition during their ultimate season (breeders e, figure 4). In the alternative approach, the data set was modified by omitting non-survivors to avoid the influence of the terminal breeding event. Thus, the new data set (set B, figure 4) included only individuals in good condition, all surviving to the next year (breeders a, b and c, figure 4). Therefore, in this data set, the survival to the next year but one of successful and unsuccessful breeders was compared. Chi-square test was used to compare survival of successful and unsuccessful performers. Tests were performed separately for each age class, since survival is age dependent (Rattiste & Lilleleht 1995).

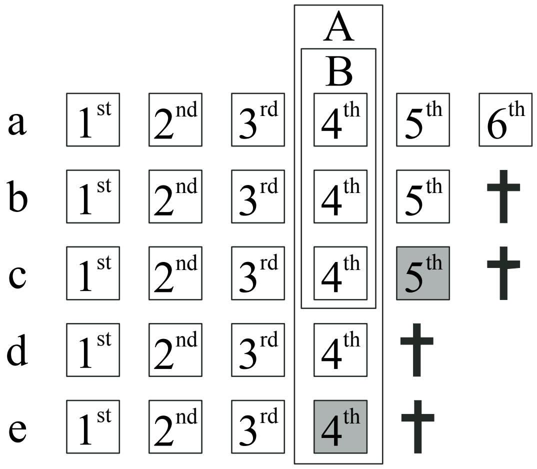

Figure 4. The two data sets for testing the survival selection hypothesis. Rows represent individual life histories, columns are breeding years. Crosses indicate death, shading points to premortal condition during the ultimate breeding season. A and B are the data sets used in the conventional and alternative tests, respectively.

There was a pronounced trend for successful breeders to enjoy a higher probability of survival to the next year in comparison with unsuccessful breeders, if the data set includes terminal breeding events (data set A). When terminal breeding events were omitted (data set B), this trend disappeared. Hence, a positive correlation in the full data set was solely based on the poor breeding success of terminal breeders and there is no convincing support for differential survival among poor and good performers. Thus, the assumptions of the selection hypothesis explaining the increase of mean reproductive performance with age could not be verified. In particular, common gulls with lower breeding success were shown not to have lower survival. There is thus no evidence of progressive elimination of poor breeders from the population.

In the longitudinal analysis, the breeding success of common gulls increased until the tenth breeding year and started to decline thereafter (figure 5a). When the terminal breeding events were omitted from the individuals' life histories, the effect of the reproductive life span on breeding success disappeared (figure 5b). Thus, birds with different life spans did not differ in their breeding success and the increase in the average reproductive success with advancing age in presenescent common gulls cannot be explained by selection effects, but rather by age-related improvements of competence and/or increased reproductive effort.

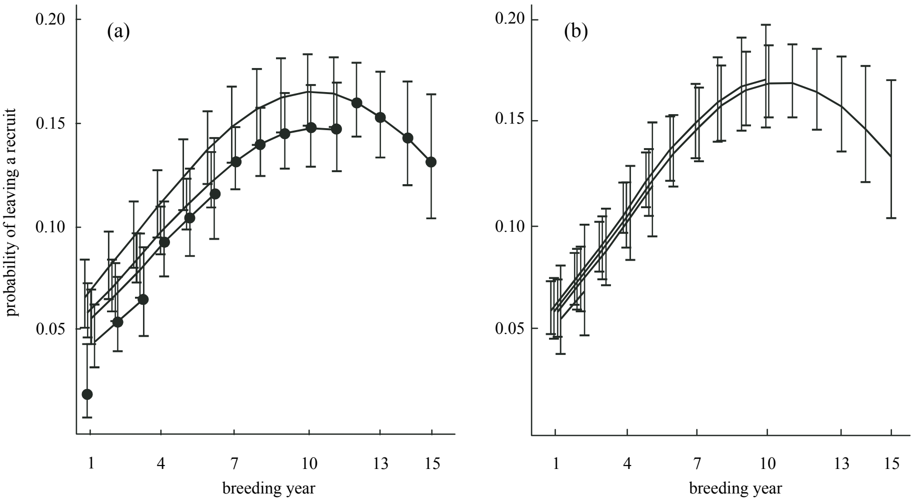

Figure 5. Breeding success of common gulls (predicted values from the model) in relation to the bird's prior breeding experience and reproductive life span according to whether life histories included terminal breeding events (a) or not (b). Curves represent the five life span categories (see Material and methods). Error bars indicate 95% CIs, filled circles point to age groups containing the terminal breeding events, sexes pooled

An important implication of the results of this analysis is methodological. If the terminal breeding event is exceptional in terms of breeding success, it cannot be used to characterize an individual's general quality, because this low success reflects the individual's worsened condition rather than its quality. Thus, one may succeed in different conclusions about differential survival of poor and good quality individuals depending on whether data sets do or do not include the terminal breeding events. More generally, this finding emphasizes the advantage of longitudinal analyses over the cross-sectional ones.

Survival of adult birds (II)

We used mark-recapture data from 16 sampling periods (1968–1983) to model the survival and recapture rates of breeding common gulls. Two samples of gulls were used in the analyses. The first data set (347 individuals) consisted of birds known to be first-time breeders when first observed in colony. The second data set (1269 individuals) contained also birds of unknown origin (unmarked before first capture).

In the first data set, we did not detect any influence of age and sex on survival, but time dependence was significant and can be explained by winter severity. In cold winters the survival was lower than in normal and warm winters (Table 1). We suspect that the age effect on survival rate remained undetected owing to sparse data.

Table 1. *Survival rates of common gulls in relation to severity of winters*

Severity of winter	Survival rate estimate	Standard deviation	95% confidence interval
Cold	0.865	0.019	0.823–0.898
Normal	0.896	0.010	0.874–0.915
Warm	0.929	0.019	0.880–0.959

In the second sample, we detected age- and time-dependent survival for both sexes. We also found differences between the sexes in recapture probability (in both samples). This was probably caused by lower site tenacity of females. Although males and females are approximately equally catchable/observable, females escaped identification more frequently due to their temporary emigration.

Wing tip pattern and pair retention (III)

Our analysis shows that the individual variation in the wing tip patterns of common gulls indicates variation in individual condition. The area of white spots on the five outermost primaries predicted the bird's future survival and divorce probabilities. Gulls with larger spots enjoyed higher survival (figure 6) and lower divorce rates (figure 7). As a consequence, their pair bond persisted longer compared to pairs with smaller spots (figure 8).

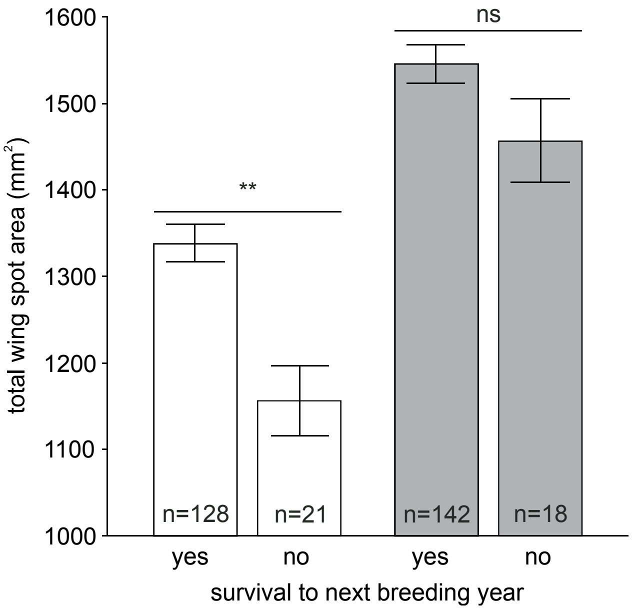

Figure 6. Survival of common gull females (white bars) and males (grey bars) to the next breeding year in relation to their white spot area. ** p = 0.002, ns nonsignificant.

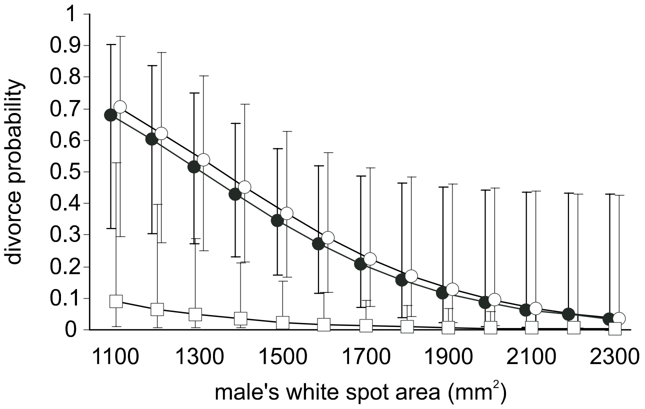

Figure 7. Divorce probability of common gulls (predicted values from the model) in relation to male’s white spot area and age composition of the pair (open circles, both mates first time breeders; filled circles, one mate first time breeder, another 6th time breeder; filled squares, both mates 6th time breeders). For better visualization only three age composition categories are shown. Error bars indicate 95% confidence intervals.

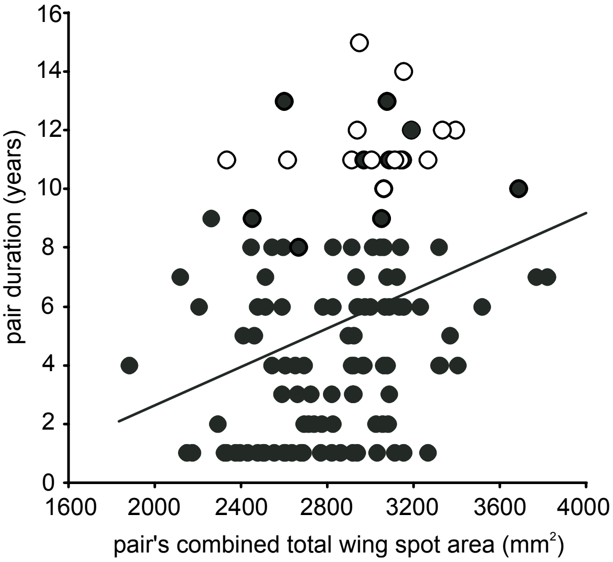

Figure 8. Pair bond duration of common gulls in relation to mates' combined white spot area. Spot areas were combined since there was no differences between sexes. Open circles indicate pairs which duration may be underestimated because mates still bred together in 2006.

Individuals with a persistent pair bond both avoided costs of pair breakage and gained pair retention benefits. Widowed and divorced individuals started to breed significantly later than birds retaining their previous mate (figure 9).

In addition, the timing of breeding of persistent pairs advanced with time not only due to mates' increasing age, but also owing to their experience together (figure 10). Hence, one of the advantages of persistent pair bond is the ability to start breeding early in the season. Consequently, it is beneficial for common gulls to rely on wing tip pattern in their mate choice.

The five outermost primaries are exchanged during autumn, when birds are migrating slowly to wintering area and at the same time are recovering from the stress of breeding effort. Thus, the burden of parental care may influence the wing tip pattern. In accordance with this hypothesis, males with fewer offspring in previous year had, indeed, smaller wing spots.

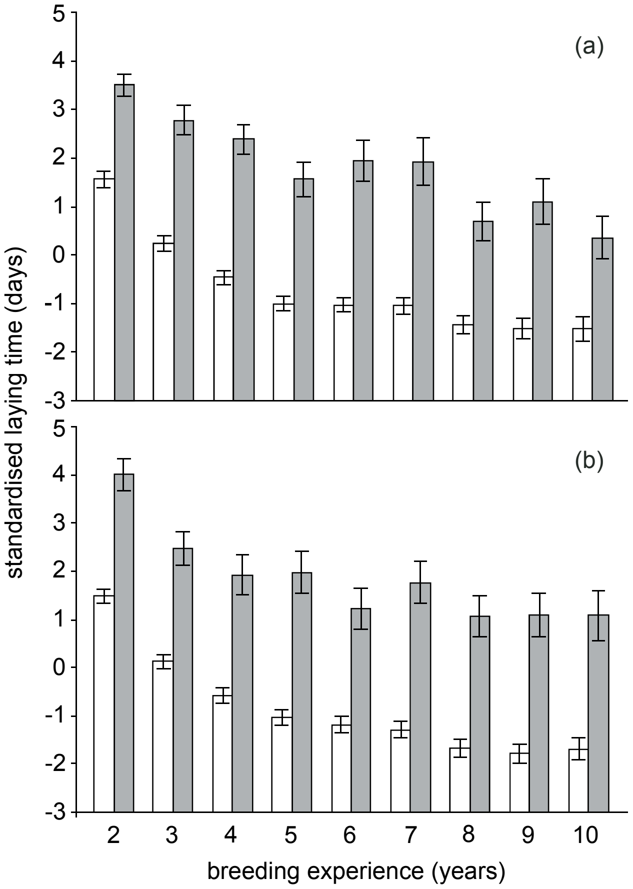

Figure 9. Laying time of common gulls in relation to the pair retention (persistent pairs: white bars; newly established pairs: grey bars) and breeding experience in (a) males and (b) females. Laying time is standardized in relation to median for particular year, i.e. smaller value corresponds to earlier laying. Error bars represent ± 1 s.e.m.

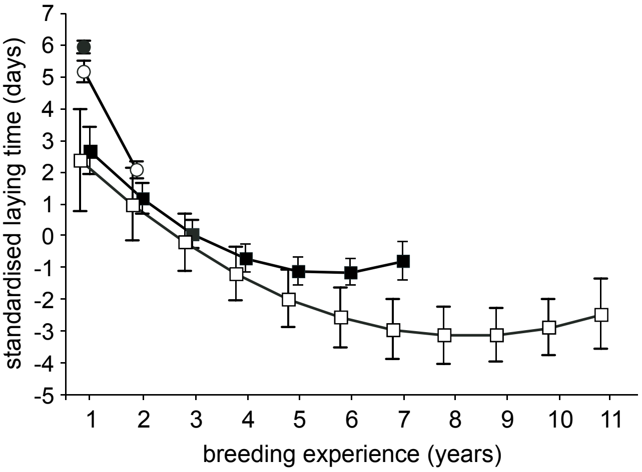

Figure 10. Laying time of common gulls (predicted values from the model) in relation to the female's breeding experience and pair duration. Laying time is standardized by subtracting median laying time for particular year, i.e. smaller value corresponds to earlier laying. For the better visualization, only the breeding pairs lasting 1 (filled circle), 2 (open circles), 7 (filled squares) and 11 years (open squares) are shown. Error bars represent ± 1 s.e.

The wing tip pattern of common gulls appeared to be highly variable, sexually dimorphic, as well as age and condition dependent. This indicates that wing spots might indeed function as a signal, revealing inter-individual variation in quality. Thus, potentially, white spot area can be used in mate choice. However, in contrast to short-lived species with low survival rates, the probability that both pair members will survive to the following season is relatively high in common gulls. Selection may therefore favour mate fidelity, since the number of available partners will be low, and this increases the cost of mate searching and reduces the likelihood of gaining a higher-quality partner. Hence, in common gulls, it pays to wait for the old partner once an individual has obtained a satisfactory mate. However, Ludwig & Becker (2006) showed that in another long-lived species, common tern (Sterna hirundo), birds will start searching for a mate immediately after arriving at the colony site without waiting for their previous mate, while keeping the option open to switch back if the missing partner returns within a given period. Thus, in spite of high pair retention, long-lived species evaluate potential mates yearly and therefore a reliable indicator trait is needed to estimate the quality of the potential mate. Our results indicate that wing tip pattern may be such a condition-dependent signal in the common gull.

Selection on the timing of laying (IV)

In order to test whether there were sex-specific effects on phenotypic laying date, we performed a Restricted Maximum Likelihood (REML) linear mixed model analysis. The breeding experience of both male and female parent affected the laying date. Apart from their respective breeding experience, male and female identity explained substantial variation in laying date (10% and 18% of the variance, respectively) illustrating that other individual-specific aspects than breeding experience affected laying date. Yearly fluctuations were substantial, explaining 34% of the variation in laying date. Despite the clear effect males have on phenotypic expression of laying date, we found no evidence of additive genetic effects in male laying date. Hence, differences in laying date across males are environmentally determined, and laying date is, on the genetic level, a sex-linked trait.

We analysed annual selection for fecundity (number of recruited offspring) and survival. There was strong evidence for fecundity and survival selection for early laying in females at both the phenotypic and genetic level. We concluded that the production of a recruit essentially requires an early start, judging from the entirely consistent direction of the fecundity selection gradients in 33 years (although not all are significant).

Comparison of the expected response based on phenotypic and genotypic values of laying dates allows verification of whether selection acts only on the genotypic component (figure 1A) or mainly on the environmental component (little or no selection on the genotypic component, figure 1B and 1C respectively). Postma (2006) showed that only the (non-standardized) selection differential on PBVs (S_{PBV} = cov[PBV, w]) provides an unbiased estimate of the selection on true breeding values (S_a). Hence, we compared S_{PBV} to the product of heritability h^2 and the phenotypic selection differential ($h^2 S_P$). In the absence of selection on the environmental deviations, and in the absence of genotype-environment interaction on the trait, $S_{PBV} = h^2 S_P$ (figure 1A).

The annual phenotypic selection differentials for fecundity were stronger (more negative) than the selection differentials on the genotypic level (figure 11A, paired t-tests: $t_{32} = 4.1$, $p = 0.0002$). This indicated that both phenotypic laying date and recruitment were affected by an environmental value (i.e. pattern of figure 1B). Merely considering phenotypic selection could, in some years, lead to an up to three-fold stronger expected response than when considering the PBVs. In contrast, there was no environmental covariance between laying date and survival (figure. 11B, $t_{32} = -0.53$, $p = 0.60$; $h^2 S_P = S_{PBV}$, pattern of figure. 1A).

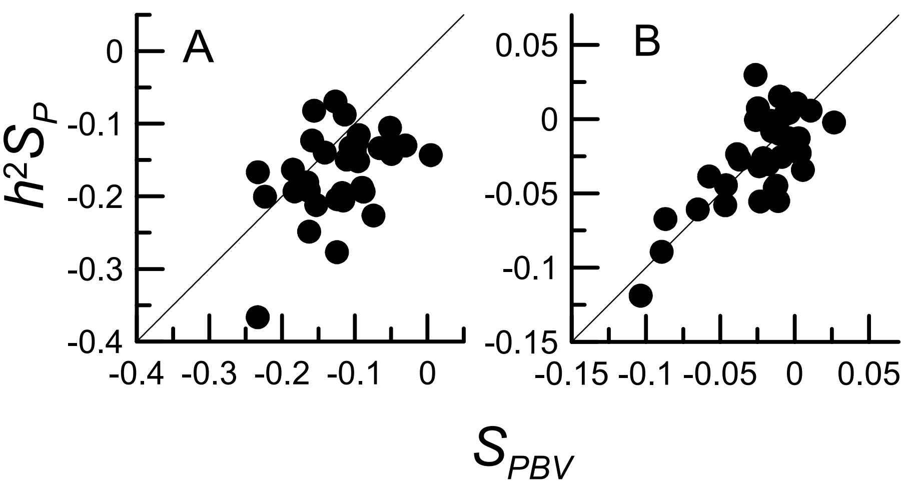

Figure 11. Comparisons between selection on the phenotypic level and the genotypic level for females' recruitment (panel A) and survival (panels B). Selection was calculated for 33 years (1968 – 2002 except 1984/1985). Plotted is the product of heritability (0.17) and the annual phenotypic selection gradient (h^2S_P) against the annual selection gradients on the PBVs (S_{PBV}). These values will correspond in the absence of an environmental covariance between laying date and recruitment or survival (c.f. figure 1), and perfect correspondence is here indicated by the diagonal line.

We found evidence that local spring temperature was involved in mediating the environmental covariance between laying date and recruitment, but not between laying date and survival. Very few studies have been able to correct for possible environmental covariances between trait and fitness when formulating their expected response (Merilä *et al.* 2001). In common gulls, years with warmer spring temperatures (prior to laying) had a higher recruitment probability. Furthermore, the environmental covariance between recruitment and laying date became stronger in warmer years. Hence, selection measured under favourable environmental conditions is also the most biased estimation of the expected response. Such a relationship is worrying for the study of evolutionary dynamics in the wild, because the quantification of selection is most powerful under favourable environmental conditions, when many offspring recruit, but possibly also most inflated.

Heritability in varying environment (V)

We classified growth conditions by using the mean head length of recruits as the classification criterion for 23 different cohorts of gulls that hatched between 1968 and 1983 and between 1986 and 1992). The underlying assumption for this classification was that the mean head length values of recruits from different cohorts would, to some extent, reflect the environmental conditions to which these cohorts were exposed during growth. This assumption was corroborated by our finding that yearly mean values of head length of 25- to 27-days-old chicks correlated positively with mean head length of recruits from the corresponding cohorts ($r = 0.68$, $n = 11$ years, $P = 0.02$).

We found that heritability and additive genetic variance estimates obtained from offspring-parent regressions and full-sib analyses differed across environments, such that estimates were higher when offspring had grown up under good environmental conditions than under poor environmental conditions ($F_{1,273} = 4.01$, $P<0.05$, homogeneity of slopes test) (Table 2).

Table 2.*Heritability (h^2) and additive genetic variance (V_A) estimates for head length in a common gull population in relation to environmental conditions during offspring growth, n = number of families. SE = standard error of h^2 estimates. Asterisks indicate that heritability estimates are significantly different from zero*

	Poor				Normal				Good			
	n	V_A	h^2	SE	n	V_A	h^2	SE	n	V_A	h^2	SE
Offspring-midparent	111	2.04	0.38	0.10***	137	1.87	0.46	0.09***	175	3.68	0.70	0.07***
Offspring-mother	141	2.06	0.53	0.16***	162	2.58	0.67	0.13***	192	3.95	0.88	0.11***
Offspring-father	136	2.00	0.39	0.15**	159	2.58	0.67	0.14***	189	3.46	0.71	0.12***
Full-sibs	19	0.64	0.27	0.43	29	3.01	0.29	0.29**	37	4.91	1.22	0.19***

**P< 0.01, ***P< 0.001

We found no significant differences in the phenotypic variance among offspring or parents in the three analysed groups, and the lower heritability estimates obtained under poor offspring growth conditions therefore cannot be ascribed to an increased environmental variance.

Further, we found no significant differences between slopes of offspring-mother and offspring-father regressions in any of the three environments. This indicates that size-related maternal or paternal effects, or effects of extra-pair fertilizations, were absent or weak.

We suggest that the different heritability and additive genetic estimates obtained in this study were a consequence of genotype-environment interactions, and that different genotypes were expressed differently in different environments (had non-parallel reaction norms) (Stearns, 1992).

The results of this analysis suggest that estimates of genetic parameters such as heritabilities and genetic correlations may vary even within relatively short time periods in natural populations because of the presence of genotype-environment interactions. If the influences of genotype-environment interactions on the phenotypic variation are large, then it follows that predictions or reconstructions of genetic responses to selection over longer time periods in spatially or temporarily heterogeneous environments might be unreliable (Mitchell-Olds & Rutledge, 1986; Turelli, 1988; Stearns, 1992).

Conclusions

This long-term individual-based study on common gulls revealed a steady increase in reproductive success until very old age. This increase cannot be explained by selection effects, since individuals with lower breeding success were shown not to have lower survival. Consequently, this gain must be ascribed primarily to age-related improvements of individual competence and/or increased reproductive effort. Pre-senescent individuals were shown to have a specifically low breeding success in their terminal breeding event. Annual survival of adult birds was age- and year-dependent. The latter was partly explained by winter severity. The size of white spots on five outermost primaries predicted the bird's future survival and divorce probabilities and hence, pair endurance capability. Gulls with larger spots enjoyed higher survival and lower divorce rates compared to birds with smaller spots. This suggests that wing tip pattern might function as a condition dependent signal, revealing individual variation in quality. One of the advantages of persistent pair bond was the ability to start breeding early in the season. The timing of breeding of firm pairs advanced with time not only due to mates' increasing age, but also owing to their experience together. Both common gull males and females had phenotypic effects on laying dates, but laying date is heritable only in females. On the phenotypic and genotypic level, early laying was under positive fecundity and survival selection in females. There was an environmental covariance between laying date and fecundity, which was driven by warmer local spring temperature leading to an earlier start in laying and an increase in offspring recruitment. This environmental covariance tended to be stronger in warmer years. The analysis of heritability of body size revealed the influence of environmental conditions during offspring growth on estimates of heritability and additive genetic variance, suggesting genotype – environment interaction be common in nature.

Summary in Swedish (Sammanfattning)

Inledning

För att förstå den kortsiktiga ekologiska och den långsikta evolutionära dynamiken hos en population krävs en ingående studie av demografiska faktorer såsom överlevnad och reproduktion, samt olika egenskapers genetiska variation och den selektion som råder på dessa egenskaper. Flertalet studier har gjorts på kortlivade arter, men det finns skäl att tro att andra förutsättningar råder hos arter som har en potentiellt lång period av reproduktion framför sig. Bra exempel på detta är parsammanhållning och erfarenhet som i andra sammanhang visats sig vara av stor betydelse för reproduktiv framgång. Denna studie har utförts på en koloni av fiskmåsar på den estländska västkusten. Material har insamlats under en period av 35 år med individmärkta fåglar. Det betyder att ett mycket stort antal enskilda individer kunnat följas från kläckning till sista livsåret. I genomsnitt häckar fiskmåsar under 5-6 år, men upp till 20 % häckar under mer än 10 år.

Frågeställningarna i denna studie är:

- finns det någon koppling mellan erfarenhet och häckningsframgång (I)?
- finns det några mönster vad gäller överlevnaden i denna population (II)?
- finns det tydliga signaler hos individer vad gäller kvalitet som häckningspartner (III)?
- finns det någon selektion på tidpunkten för reproduktion, och finns det någon genetisk variation som kan ge en evolutionär respons (IV)?
- finns det någon ärftlighet hos morfologiska egenskaper och hur varierar den med miljön (V)?

Studie I

Ett välkänt mönster hos fåglar är att häckningsframgången ökar med antalet häckningar (ålder). Tre olika förklaringar har föreslagits för detta fenomen: 1) individer med dålig häckning har även en dålig överlevnad, dvs det finns en generell koppling mellan en individs kvalitet och deras överlevnad och häckning. Genom att dessa individer successivt försvinner återstår bara individer som både överlever bra och har en god häckningsframgång. 2) Häckningsframgång är relaterad till erfarenhet. 3) Individer optimerar sin reproduktiva insats genom att öka häckningsinsatsen när erfarenheten är störst.

Det finns två sätt att testa detta: dels genom att göra en tvärsnittsanalys där relationen mellan ålder, häckningsframgång och överlevnad studeras vid ett tillfälle, och dels genom att följa ett antal individer över hela deras levnadstid och analysera överlevnad, häckningsframgång och ålder. Detta gjordes på data från fiskmåskolonien. Det fanns mycket riktigt en koppling mellan överlevnad och häckningsframgång. Detta var emellertid enbart ett resultat av att fåglar under sin sista häckning även hade en mycket dålig häckningsframgång. Om man bortser från det sista året försvinner kopplingen mellan häckningsframgång och överlevnad. Individer som av någon anledning, såsom sjukdom, startar en häckning i dålig kondition misslyckas oftare och överlever sedan inte till nästa år. Förklaringsmodell 1) kan därför förkastas för denna art. Data visar att häckningsframgången ökar stadigt till det tionde häckningsåret för att sedan avta. Studien visar dessutom på betydelsen av longitudinella studier där enskilda individer följs under sin livstid.

Studie II

En viktig demografisk faktor är överlevnad. Genom att analysera fångst och återfångst av märkta individer kan överlevnaden mellan år uppskattas med hjälp av kraftfulla statistiska metoder. I denna studie analyserades två grupper av fåglar som ringmärkts som ungar; dels de som häckade för första gången, och dels de som häckat tidigare. Inom bägge grupperna finns en åldersvariation eftersom ålder för första häckning varierar mellan individer. Överlevnaden var generellt hög i bägge grupperna (86 % eller högre). I gruppen av förstagångs-häckare fanns det ingen skillnad mellan olika åldrar eller mellan könen, men däremot en kraftig effekt av medeltemperaturen under vintern. Kalla vintrar var överlevnaden i snitt 86.5 % medan under varma vintrar var överlevnaden 92.9 %. I gruppen av fåglar som häckat tidigare fanns en klar skillnad mellan olika åldersklasser och mellan år, liksom mellan könen.

Studie III

Hos långlivade arter som fiskmåsen finns det en klar koppling mellan häckningsframgång och erfarenhet. Det lönar sig därför att försöka hitta de individer som har störst erfarenhet, men detta kan bara fungera om det finns en signal som ärligt visar en individs ålder och kvalitet. En sådan signal är storleken på de vita vingfläckarna som varierar mellan könen och mellan åldersklasser. Vingspetsarna är normalt svarta eftersom melanin ger stadga och vingarna. Det är därför kostsamt att ha stora vita fläckar, och dessa kan därför fungera som en ärlig signal på fenotypisk kvalitet.

Det finns en tydlig koppling mellan hur länge ett par häckat tillsammans och deras häckningsframgång. Överlevande honor har större vita vingfläckar än de som dog under en vinter. Sannolikheten för att ett par skulle bryta upp till nästa häckningssäsong sjunker med storleken på de vita vingfläckarna hos hanen, speciellt för de par som häckar för första gången. En fördubbling av hanens vingfläckstorleken minskar sannolikheten för en skillsmässa efter första häckningen dramatiskt, från 70% till under 10%. Antalet år ett par häckar tillsammans ökar med parets sammanlagda yta av de vita fläckarna. Studien visar därför att storleken på de vita vingfläckarna är en ärlig signal av olika individers förmåga att häcka framgångsrikt.

Studie IV

Den mest kraftfulla mekanismen för evolutionära förändringar är selektion. Selektionen verkar på fenotypnivå eftersom det är individuella fenotyper som överlever och reproducerar sig. Standardmetoderna för att mäta selektion handlar därför om att uppskatta skillnad i överlevnad och reproduktion mellan individer. Utifrån dessa mått på selektionens intensitet är det därefter möjligt att uppskatta hur stor den evolutionära förändringen blir genom enkla medel.

Det finns dock ett problem och det är att en fenotyp är ett resultat av både gener och miljö, och det går att särskilja tre fall där den förväntade evolutionära responsen skiljer sig beroende på den relativa betydelsen av gener och miljö. Om vi, till exempel, har ett resultat som visar att reproduktiv framgång är relaterat till när häckningen påbörjas, kan detta ha tre olika orsaker: A) det finns en genetisk bakgrund till variationen i äggläggningstid och förmåga att föda upp ungar. I detta fall leder selektionen till ett evolutionärt resultat eftersom den genetiska variation är systematisk, men inte den miljömässiga. B) både gener och miljö påverkar så att det finns en genetisk bakgrund till variationen i äggläggningsdatum, men även en likadan miljöbetingad variation. Det beytder att en evolutionär förändring är trolig, men inte så stark som kan förväntas utifrån den selektion som uppmätts. C) All systematisk variation i äggläggningstider är miljörelaterad, men inte genetisk. I detta fall leder selektionen inte till någon evolutionär respons.

Genom att studera äggläggningstiden vid 10 740 äggläggningstillfällen för 2078 hanar och 2123 honor har jag uppskattat den genetiska och miljörelaterade variationen i äggläggning, och selektionen på fekunditet och överlevnad med hjälp av kraftfulla statistiska metoder. Resultaten visade att både hanens och honans fenotyp påverkar datum för första ägg, men att genetisk variation bara finns hos honor. Ett tydligt mönster är selektion för tidig äggläggning hos honor eftersom det leder till fler ungar som i sin tur reproducerar sig. Denna selektion finns både på den fenotypiska och den genetiska nivån hos honor. Det finns dock en koppling mellan temperaturen under ankomsten till häckningslokalen på våren och äggläggningsdatum och därmed en koppling mellan häckningsframgång och temperatur. Denna koppling var starkare under varma vårar, vilket betyder att miljöeffekterna är olika under olika år. En viktig slutsats från denna studie är att en studie av enbart fenotypisk selektion kan leda till en överskattning av den evolutionära responsen, och att denna överskattning är olika under olika miljöbetingelser.

Studie V

Morfologiska egenskaper har ofta en hög ärftlighet och kan därför förväntas svara evolutionärt på selektion för en ändring av storlek. För att studera detta analyserades ärftligheten hos skall-längden hos fiskmåsar. Ärftligheten (h2) var som väntat hög, och på den nivå som hittats hos många andra arter. Vi hittade inga tecken på en skillnad i ärftlighet mellan könen, vilken tyder på att varken maternella eller paternella effekter inte har någon större betydelse hos denna egenskap i denna population. Däremot var ärftlighetsmåtten beroende av miljön så att under goda år var ärftligheten hög, medan den var låg under dåliga år. Orsaken till detta är att den additiva genetiska variationen var lägre under dåliga år, och högre under bra år. Detta i sin tur kan förklaras med en interaktion mellan genotyper och miljö så att uttrycket av den genetiska variation skiljer mellan individer beroende på miljön. Detta är i linje med resultaten i Studie IV som visar att förutsägelser om evolutionär respons givet en viss selektion måste ses i termer av den omgivande miljön.

Slutsatser

Denna avhandling visar att den ekologiska dynamiken hos en långlivad art som fiskmåsen beror på en komplex interaktion mellan överlevnad, partnerval och reproduktion. Den evolutionära dynamiken är dessutom strakt beroende på rådande miljöfaktorer och enkla förutsägelser är svåra att göra utan ingående studier av variation, ärftlighet och selektion. En annan viktig slutsats är betydelsen av longitudinella studier inom evolutionär ekologi.

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