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A silver spoon for a golden future: long-term effects of natal origin on fitness prospects of oystercatchers (*Haematopus ostralegus*)

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Summary

1. Long-term effects of conditions during early development on fitness are important for life history evolution and population ecology. Using multistrata mark–recapture models on 20 years of data, we quantified the relation between rearing conditions and lifetime fitness in a long-lived shorebird, the oystercatcher (*Haematopus ostralegus*). We addressed specifically the relative contribution of short- and long-term effects of rearing conditions to overall fitness consequences.

2. Rearing conditions were defined by differences in natal habitat quality, in which there is a clear dichotomy in our study population. In the first year of life, fledglings from high-quality natal origin had a 1·3 times higher juvenile survival. Later in life (age 3–11), individuals of high-quality natal origin had a 1·6 times higher adult prebreeder survival. The most striking effect of natal habitat quality was that birds that were reared on high-quality territories had a higher probability of settling in high-quality habitat (44% vs. 6%). Lifetime reproductive success of individuals born in high-quality habitat was 2·2 times higher than that of individuals born in low-quality habitat. This difference increased further when fitness was calculated over several generations, due to a correlation between the quality of rearing conditions of parents and their offspring.

3. Long-term effects of early conditions contributed more to overall fitness differences as short-term consequences, contrary to common conceptions on this issue.

4. This study illustrates that investigating only short-term effects of early conditions can lead to the large underestimation of fitness consequences. We discuss how long-term consequences of early conditions may affect settlement decisions and source–sink population interactions.

Key-words: early conditions, habitat selection, lifetime reproductive success, parental effects, multistrata capture–recapture models.

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Introduction

The long-term consequences of conditions during early development for fitness are important for life history evolution, population ecology and the interface between them (Lindström 1999; Cam, Monnat & Hines 2003). Early conditions are likely to influence offspring quality, which is an important factor in main life history trade-offs (Stearns 1992). For example, long-term effects of early conditions shift the optimal solution of the trade-off between quantity and quality of offspring towards fewer offspring of higher quality. In an ecological context, effects of early conditions may amplify a source–sink population structure when breeders in good habitats produce many offspring that additionally have higher fitness prospects. Effects of early conditions on life history traits can also provide feedback on population dynamics. For example, early conditions can affect the

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prospects of entire cohorts, which may have delayed consequences for population dynamics (Albon, Clutton-Brock & Guinness 1983; Sæther 1997); condition-dependent dispersal is important for meta-population dynamics (Ims & Hjermann 2001).

Conditions during early life can vary as a result of differences in parental quality and environmental quality; the latter are partly under parental control. For example, parental habitat selection affects the spatial environment in which offspring are reared; a mother's choice of date of birth affects the temporal environment in which offspring are reared. Parental and environmental quality are therefore linked intricately and probably often positively intercorrelated (e.g. van de Pol *et al*. 2006).

Favourable rearing conditions, i.e. being raised with a 'silver spoon' (Grafen 1988), are often beneficial throughout life, but are thought to be most pronounced during early life stages (Lindström 1999; Metcalfe & Monaghan 2001). Two hypotheses may explain why the effects of early conditions are most pronounced early in life. First, the environmental stochasticity that individuals experience during life accumulates and this decreases the potential for long-term effects of early conditions. Secondly, selection gradients of fitness components usually become less strong during the course of life (Charlesworth 1980; Caswell 2001). Consequently, parents can expect a higher fitness payoff by improving conditions that enhance the short-term fitness prospects of offspring than by investing that same effort in improving early conditions that pay off later in life.

Many studies report 'silver spoon' effects on juvenile survival (e.g. Tinbergen & Boerlijst 1990; Magrath 1991; Green & Cockburn 2001; Perrins & McCleery 2001), natal dispersal (e.g. van der Jeugd 2001) and adult morphology (e.g. Boag 1987; Gustafsson, Qvarnström & Sheldon 1995; de Kogel & Prijs 1996). In addition, several studies suggest that early conditions can also have long-term consequences on fitness components, such as adult survival before recruitment (Harris *et al*. 1994; Cam *et al*. 2003) and recruitment probability (Reid *et al*. 2003). However, less is known about the long-term consequences of early conditions on fitness components during the reproductive stage, such as breeder survival (Perrins & McCleery 2001), quality of the acquired breeding habitat (Verhulst, Perrins & Riddington 1997) and reproductive success (Gustafsson & Sutherland 1988; Haywood & Perrins 1992; Visser & Verboven 1999).

When investigating the ecological and evolutionary consequences of early conditions, cost and benefits should be calculated in terms of fitness. Fitness measures are calculated over (at least) a lifetime [e.g. lifetime reproductive success (LRS), finite population growth rate (λ)] and they are the combined result of many individual fitness components (early as well as late in life). For logistic reasons, most studies investigate only one or a few fitness components. Consequently, little is known about the relative importance of short- and long-term consequences of early conditions on fitness. Integrating all fitness components into one fitness measure is also important because early conditions do not always affect all fitness components positively (e.g. King 2002; Olsson & Shine 2002).

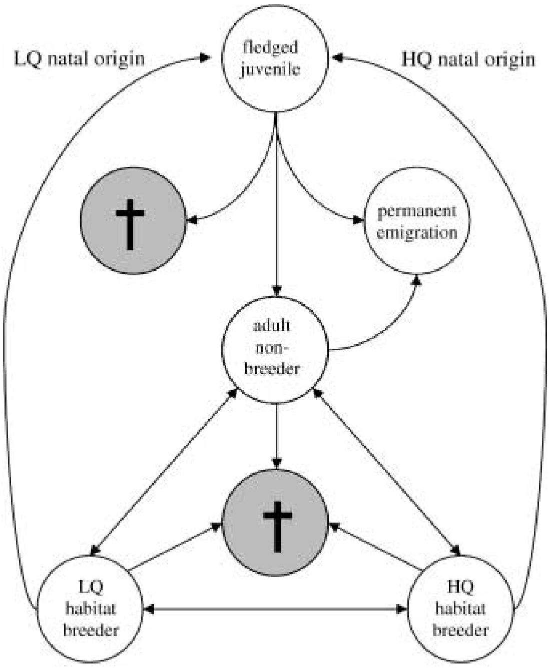

Fig. 1. Schematic overview of the life cycle stages of an oystercatcher, which are used in the multistrata mark–recapture analysis as well as the stage-structured population models. LQ: low-quality habitat; HQ: high-quality habitat.

In this paper we use data from a 20-year study to quantify and compare the contribution of short- and long-term effects of early conditions on the fitness of oystercatcher (*Haematopus ostralegus* L.) offspring. In coastal breeding oystercatcher populations there is usually a clear dichotomy in habitat quality, based on the nesting location relative to the foraging area (Safriel, Ens & Kaiser 1996). Some parents can take their chicks to the food, because breeding and feeding territory are adjacent. Other parents have to bring the food to their chicks, because the breeding and feeding territory are segregated spatially. Parents that can escort their chicks to the food consistently produce two to three times more fledglings per year, because transporting food to the chicks is costly (Ens *et al*. 1992). Early conditions in oystercatcher are therefore characterized by the habitat type in which an individual is reared. However, as natal habitat quality is probably linked intricately with parental quality (van de Pol *et al*. 2006) we prefer to use the term natal origin, which encompasses both an environmental and parental (genetic and non-genetic) component of early conditions.

We estimated the fitness consequences associated with the natal origin of offspring by calculating the effects of natal origin on juvenile survival and adult survival, recruitment probability, as well as on their subsequent breeding career (Fig. 1). We combined fitness components to estimate fledgling fitness prospects (LRS and λ). Subsequently, using stage-structured population models, we compared the sensitivity of fitness to long-term and short-term effects of early conditions. Finally, we discuss how long-term effects of natal origin affect life history evolution (settlement decisions) as well as population ecology (source–sink population interactions).

Methods

STUDY POPULATION

Oystercatchers were studied from 1985 to 2004 on the Dutch Wadden Sea island of Schiermonnikoog (53°29′ N 6°14′ W). In this population, oystercatchers breed on the salt marsh and are dependent on intertidal mudflats for their food. Breeding pairs stake out their feeding and nesting territory, facilitating location of territory boundaries (Heg *et al*. 2000b). Following earlier studies, we designated territories with adjacent feeding and nesting areas as high quality (HQ) habitat and territories with spatially separated feeding and nesting areas as low quality (LQ) habitat (Ens, Weissing & Drent 1995; Heg & van der Velde 2001).

All breeding birds and fledglings were colour-marked individually in the main study area; a large surrounding area was visited annually to locate new recruits (see Heg *et al*. 2000b for map). Age of first reproduction is high (median 7, range 3–11 years), therefore we restricted all analysis to fledglings born in 1985–96, which were followed from 1985 to 2004. By 2004, all individuals of these cohorts had either settled or had not been seen for several years and were presumed dead. Sex of adult birds was determined on the basis of DNA analysis (Heg *et al*. 2000a), adult morphology (Zwarts *et al*. 1996) and copulation behaviour (Heg *et al*. 1993); sex of most juvenile birds was unknown until adulthood.

JUVENILE SURVIVAL AND DISPERSAL

Young fledge on average 30 days after hatching (Kersten & Brenninkmeijer 1995). Until the age of 3 years (hereafter called 'adulthood') juveniles retain their juvenile plumage. Information from re-sightings and dead recoveries suggests that juveniles have low site fidelity and move around the Wadden Sea. After 3 years, many juveniles returned to the study area and were observed repeatedly in subsequent years (Kersten & Brenninkmeijer 1995).

Survival of juveniles born from 1985 until 1996 was analysed using dead recoveries collected by the Dutch Ringing Centre. By comparing survival until adulthood based on dead recoveries from all over North-western Europe with the number of birds re-sighted locally at adulthood ('local survival') we estimated permanent juvenile emigration (Fig. 1). We adopted the same model structure as in a previous study on dead recovered oystercatchers (Nève & van Noordwijk 1997), in which it was shown that first- and second-year survival was lower than adult survival and that adult survival and reporting probability were dependent on winter severity. Reporting rates of dead colour-ringed oystercatchers were high (24%) in most years with mild winters and even higher in years with severe (1986, 1996 and 1997) winters (Camphuysen *et al*. 1996; Nève & van Noordwijk 1997).

ADULT SURVIVAL, DISPERSAL, RECRUITMENT AND BREEDING CAREER

Adult oystercatchers usually occupy the same territory from year to year with the same mate (Heg, Bruinzeel & Ens 2003). Non-breeders join communal roosts (Heg *et al*. 2000b). Annual determination of social status (HQ or LQ habitat breeder or non-breeder) was based on observations during the breeding season at the breeding grounds and at roosts (average 30 observations/individual/year). Virtually all surviving breeders and non-breeders were re-sighted each year, with the exception of non-breeders from 1997 until 2004 due to less frequent checking at roosts.

Adult survival and transition probabilities between the state of non-breeder, breeder in LQ habitat and breeder in HQ habitat (i.e. recruitment, movement between breeding habitat and territory loss) were all estimated in one combined model, using multistrata mark–recapture models based on live re-sightings (as in Fig. 1). By using live local re-sightings to estimate adult survival, permanent adult emigration will result in an underestimation of survival. In principle this adult dispersal fraction can be quantified by using information from dead recoveries from a larger area. However, given the low number of juveniles that survived until adulthood, the number of dead recovered adults was too few to incorporate this information into the models. Analysis of a larger data set, including individuals ringed as adults, suggested that a small fraction of adult non-breeders of both sexes emigrated, but breeders did not (van de Pol, unpublished data).

Capture–recapture analyses were carried out using MARK (Cooch & White 2004). Model selection was conducted using Akaike's information criteria corrected for sample size (AICc; Akaike 1973). Parameter estimates were calculated using model averaging (Burnham & Anderson 2002), which combines estimates of all models in one overall estimate using differences in model support (AICc) to determine weight. Estimates from years with mild and severe winters were combined in one weighted parameter estimate. Goodness-of-fit analyses were performed using a median c-hat approach on a reduced model with no differences between years and natal origin (Cooch & White 2004). There were no indications for lack of fit (c = 1·21).

The local natal dispersal distance (m) was defined as the distance between the centres of the natal territory and the territory in which the individual first recruited. To investigate whether recruits avoided or congregated near their natal territory, the observed settlement pattern

Table 1. Estimates of fitness components and LRS of fledglings born in low-quality and high-quality territories. †Values between brackets refer to the estimates for the 'emigration scenario' (see text)

	Quality natal origin	
Fitness component	Low (*N* = 107)	High (*N* = 203)
Survival from fledging until adulthood	31·9%	41·2%
1st-year survival	43·7 ± 6·6%	60·5 ± 4·8%
2nd-year survival	74·3 ± 9·0%	72·0 ± 7·4%
3rd-year survival	98·2 ± 2·2%	94·5 ± 8·9%
Returned to study area at adulthood	30·8% (= 33/107)	41·4% (= 84/203)
Recruited as breeder	39·4% (= 13/33)	54·8% (= 46/84)
Recruited in low quality habitat	92·3% (= 12/13)	67·4% (= 31/46)
Recruited in high quality habitat	7·7% (= 1/13)	32·6% (= 15/46)
Age of first reproduction (years)	6·4 ± 0·6	6·8 ± 0·3
Life span of surviving juveniles (years)	13·5 (17·3†)	17·1
Non-breeding life span (years)	9·4 (11·6†)	10·5
Breeding life span (years)	4·1 (5·7†)	6·6
Breeding life span in low quality habitat (years)	2·7 (3·8†)	3·8
Breeding life span in high quality habitat (years)	1·4 (1·9†)	2·8
LRS from fledging (no. of fledged offspring)	0·13 (0·17†)	0·28

Table 2. Results of juvenile survival analysis based on dead recoveries. S^1, S^2, S^3, S^A refer to 1st-year, 2nd-year, 3rd-year and adult annual survival, respectively. R refers to the reporting probability, which was equal among all age classes. (n) refers to natal origin (w) refers to winter severity and (r) refers to either individuals ringed as fledgling or ringed as adult. Individuals ringed as adults were included to improve parameter estimates

Model	ΔAICc	AICc weights	No. Par.	Deviance
1. $S^1(n),S^2,S^3,S^A(w),R(w)$	0·00	0·38	8	140·6
2. $S^1(n),S^2(n),S^3,S^A(w),R(w)$	0·96	0·23	9	139·5
3. $S^1(n),S^2(n),S^3(n),S^A(w),R(w)$	2·15	0·13	10	138·7
4. $S^1,S^2,S^3,S^A(w),R(w)$	2·18	0·13	7	144·9
5. $S^1(n),S^2(n),S^3(n),S^A(n \times w + r),R(w)$	2·88	0·09	14	133·2
6. $S^1(n \times w),S^2(w),S^3(w),S^A(w),R(w)$	4·60	0·04	12	137·0

was compared with a random settlement pattern generated by taking 5000 bootstrap-replicates (Adams & Anthony 1996). Breeding dispersal is on the same scale as local natal dispersal (Bruinzeel 2004).

STAGE-STRUCTURED POPULATION MODELS

Stage-structured population matrix models were constructed based on the estimated demographic parameters (Caswell 2001). These models were used to quantify the finite population growth rate (λ) and thereby allowed the quantification of the strength of phenotypic selection on input parameters (fitness components early and late in life). Such selection gradients (also called sensitivities) are calculated as the partial derivative of a specific parameter to λ (Hamilton 1966; Caswell 2001). In addition, stage-structured models were used to quantify the fitness differences of fledglings of LQ or HQ natal origin in terms of reproductive value (RV). RV is a relative measure of the contribution of different groups to λ. RVs account for the fact that timing of reproduction during a lifetime affects fitness when populations change in size, while LRS ignores this.

Results

JUVENILE SURVIVAL AND DISPERSAL

Juveniles of HQ natal origin were 1·3 times more likely to survive their first year than juveniles of LQ natal origin (Table 1). Because this analysis was based on recoveries of dead birds throughout the Wadden Sea and beyond, it is unlikely that this survival difference can be attributed to differential dispersal. Models with second-year (model 2, Table 2) or third-year (model 3, Table 2) survival dependent on natal origin received less support from the data than the model with only first-year survival dependent on natal origin (model 1, Table 2). Multiplying first-year to third-year survival we estimated that a total of 31·9% of fledglings of LQ natal origin and 41·2% of fledglings of HQ natal origin survived until adulthood (Table 1). Return rates of juveniles, based on individuals seen alive in the study area at adulthood, were remarkably close to these estimates (mean difference 0·6%, Table 1). This suggests that practically all surviving fledglings returned to the study area (i.e. no permanent juvenile emigration).

Table 3. Results of multistrata analysis based on re-sightings from 1988 to 2004. S refers to annual adult survival probability; $\Psi^{NB,LQ}$ refers to transitions from non-breeder state (NB) to low-quality habitat breeder state (LQ), and so forth. The annual re-sighting probability for all breeders was constant in all years ($P^{LQ} = P^{HQ} = 0{\cdot}99$). †$P^{NB}$(y) refers to a constant re-sighting probability (0·99) for the years 1988–96 and variable re-sighting probabilities for the period 1997–2004 (between 0·5 and 0·9). ‡$\Psi^{LQ,HQ}$ did not depend on natal origin (n) in severe winters, therefore we modelled $\Psi^{LQ,HQ}$ to depend on natal origin in mild winters (w_{mild}) only

Model	ΔAICc	AICc weights	No. Par.	Deviance
1. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	0·00	0·19	33	903·4
2. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(w)$, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	0·43	0·15	32	906·0
3. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(n \times w)$	0·61	0·14	35	899·6
4. $S^{NB}(w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	0·65	0·14	31	908·4
5. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	0·66	0·14	31	908·4
6. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w)$, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	2·17	0·06	34	903·4
7. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(n \times w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	2·59	0·05	35	901·6
8. $S^{NB}(n \times w)$, $S^{LQ}(n \times w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	2·92	0·04	35	901·9
9. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(n \times w)$, $\Psi^{HQ,LQ}(w)$	3·65	0·03	35	902·7
10. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(n \times w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	3·73	0·03	35	902·8
11. $S^{NB}(n \times w)$, $S^{LQ}(w)$, $S^{HQ}(n \times w)$, $P^{NB}(y)$†, $P^{LQ} = P^{HQ}$, $\Psi^{NB,LQ}(w)$, $\Psi^{NB,HQ}(n \times w)$, $\Psi^{LQ,NB}(w)$, $\Psi^{LQ,HQ}(n \times w_{mild} + w)$‡, $\Psi^{HQ,NB}(w)$, $\Psi^{HQ,LQ}(w)$	4·23	0·02	35	903·3

The sex of most individuals could be determined only when they returned as adults; therefore we could not test directly for sex-dependent juvenile survival. However, the sex ratio among adults that returned to the study area was male-biased (60% males, binomial test: $n = 117$, $P = 0{\cdot}042$). If we assume that there is no permanent juvenile emigration and the fledgling sex ratio is unity (cf. Heg *et al.* 2000a; based on one cohort), this suggests that survival until adulthood was 1·5 times higher in males compared to females (males: 45·3%; females: 30·4%).

ADULT SURVIVAL, DISPERSAL, RECRUITMENT AND BREEDING CAREER

Individuals of HQ natal origin that survived until adulthood were 1·4 times more likely to recruit in the breeding population during the remainder of their life (HQ: 54·8%, LQ: 39·4%; Table 1). Furthermore, recruits of HQ natal origin were 4·1 times more likely to recruit directly into HQ habitat (15/46 = 33%) compared to recruits of LQ natal origin (1/13 = 8%). This difference was not due to low sample sizes, because when recruits born in areas surrounding the main study area were included the quantitative difference remained (HQ natal origin: 27/62 = 44%, LQ natal origin: 1/18 = 6%). Thus, the effects of natal origin persisted many years after fledging, because median age at first recruitment was 7 years. Age at first recruitment was independent of natal origin (HQ: 6·8 ± 0·6, LQ: 6·4 ± 0·3, $F_{1,59} = 1{\cdot}52$, $P = 0{\cdot}22$) and of sex (♂: 6·9 ± 0·3, ♀: 6·3 ± 0·4, $F_{1,59} = 1{\cdot}30$, $P = 0{\cdot}26$).

Territory loss and territory switches after first recruitment occur regularly, which may involve promotion from LQ to HQ habitat (Fig. 1). Therefore we analysed annual transition probabilities between status categories and adult survival probabilities using multistrata models. This analysis showed that the higher probability for individuals of HQ natal origin to ever recruit resulted from both a higher annual probability of settling in HQ habitat as well as a lower annual mortality as non-breeder (Table 3, Fig. 2a vs. Fig. 2b). Non-breeders of HQ natal origin were 2·7 times more likely each year to acquire a territory in HQ habitat (HQ: 4·9%, LQ: 1·8%), but annual settlement probability to LQ habitat was independent of natal origin (HQ: 8·7%, LQ: 8·7%). Non-breeders of HQ natal origin had a 1·6 times lower annual mortality (7·8%) than non-breeders of LQ natal origin (12·2%). Possibly, the high mortality of non-breeders of LQ natal origin partly reflects permanent adult emigration, as we have indications that some adult non-breeders are not completely site-faithful (van de Pol, unpublished data).

Transition probabilities of breeders also tended to depend on natal origin (Table 3, Fig. 2). Once recruited in LQ habitat, individuals of HQ natal origin rarely moved from LQ to HQ habitat (0·8% annually), indicating a fixed habitat selection strategy (Fig. 2a). However, individuals born and settled in LQ habitat had a substantial chance (4·2% annually) of promoting to HQ

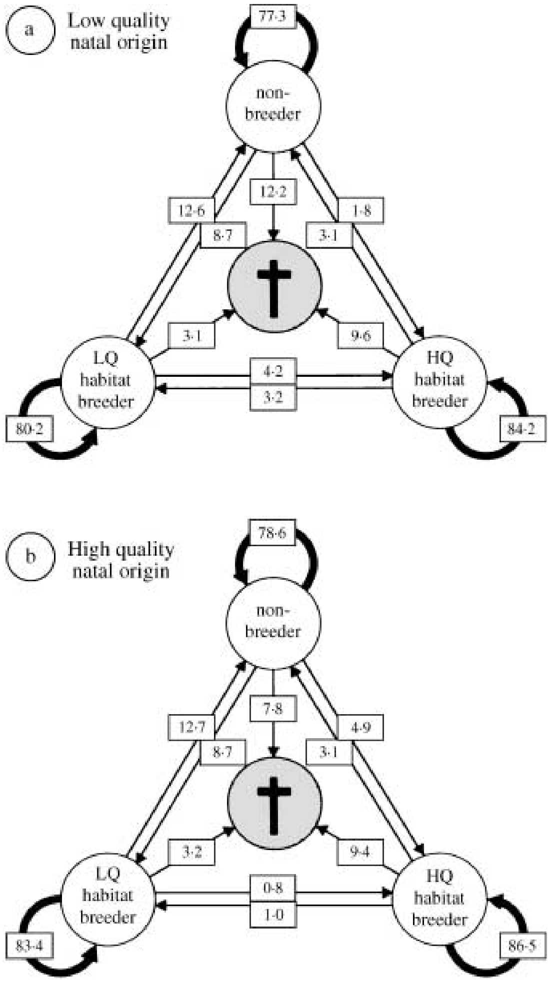

Fig. 2. Transition probabilities (%) between different life cycle stages of individuals from (a) low-quality and (b) high-quality natal origin as estimated using multistrata mark–recapture analysis. Estimates are based on (a) 84 individuals with 635 individual years and (b) 33 individuals with 201 individual years. Thin arrows represent parameters estimated in the models (Table 2); thick arrows represent parameters calculated from the estimated parameters.

habitat (Fig. 2b). Thus, for individuals of LQ natal origin the recruitment in LQ habitat can serve potentially as a stepping stone for acquiring a HQ habitat. The annual transition probability from HQ to LQ habitat was also lowest for birds of HQ natal origin (HQ: 1·0%, LQ: 3·2%; Fig. 2), supporting the idea of a fixed habitat selection strategy. However, modelling movement from HQ to LQ habitat dependent on natal origin does not result in higher model support (model 3 vs. model 1, Table 3). Interpretations of the estimated transition probabilities of breeders require caution, as they are based on relatively few individuals, which were observed repeatedly in many years. None the less, given the chosen methodology of model selection and model averaging, the estimates presented in Fig. 2 represent the most parsimonious description of the data.

Natal origin did not affect the survival of breeders in either HQ (model 11 vs. model 1) or LQ habitat (model 8 vs. model 1). However, independent of natal origin, the annual probability of dying as a breeder in HQ habitat (9%) was much higher than the probability of dying as a breeder in LQ habitat (3%). Territory loss in HQ and LQ habitat was independent of natal origin (Table 3, Fig. 2). Sex of a bird did not affect any of the transition or survival probabilities (results not shown).

Table 4. Sensitivities and elasticities of λ to the input parameters of the population model (model 1, Appendix I). Sensitivities reflect the absolute change in λ as a result of a small absolute change in a matrix element (a_{ij}) and are a measure for the strength of phenotypic selection gradients. Elasticities are proportional sensitivities; elasticities sum up to 100% and therefore can be interpreted as relative contributions to λ. Parameter abbreviations follow Tables 2 and 3. †Although S^{NB}, S^{LQ} and S^{HQ} are not matrix elements, their sensitivities can be estimated if we replace $\Psi^{NB,NB}$ by the equivalent $1 - \Psi^{NB,LQ} - \Psi^{NB,HQ} - (1 - S^{NB})$, and so forth

Life stage	Parameter a_{ij}	Sensitivity $\partial\lambda/\partial a_{ij}$	Elasticity $(a_{ij}/\lambda)\ (\partial\lambda/\partial a_{ij})$	
Juvenile	S^1	0·035	2·0%	6·0%
	S^2	0·026	2·0%	
	S^3	0·020	2·0%	
Non-breeder	$\Psi^{NB,NB}$ (S^{NB}†)	0·343 (0·344†)	28·2%	34·2%
	$\Psi^{NB,LQ}$	0·495	4·5%	
	$\Psi^{NB,HQ}$	0·470	1·5%	
Breeder	$\Psi^{LQ,LQ}$ (S^{LQ}†)	0·376 (0·337†)	32·6%	59·8%
	$\Psi^{LQ,NB}$	0·261	3·5%	
	$\Psi^{LQ,HQ}$	0·357	0·8%	
	$\Psi^{HQ,HQ}$ (S^{HQ}†)	0·220 (0·257†)	19·7%	
	$\Psi^{HQ,NB}$	0·160	0·5%	
	$\Psi^{HQ,LQ}$	0·231	0·5%	
	F^{LQ}	0·118	0·8%	
	F^{HQ}	0·073	1·2%	

SENSITIVITIES OF λ TO FITNESS COMPONENTS EARLY AND LATE IN LIFE

The population growth rate of the stage structured population matrix model without differences between natal origin was λ = 0·954 (model 1, Appendix S1). This suggests that population size declined 4·6% annually (ignoring possible immigration and emigration), comparable to the decline in breeding numbers actually observed (4·5%; Bruinzeel 2004), also suggesting that our estimates of life-history parameters were consistent. Phenotypic selection on fitness components late in life was stronger than on fitness components early in life (Table 4). Sensitivities were strongest for settlement probabilities of non-breeders, followed by transition probabilities of breeders, fecundity and juvenile survival. Although sensitivities are used in the calculation of evolutionary scenarios, dimensionless elasticities are more useful for comparing the relative contribution of different demographic parameters to λ, also between species. Fitness components in the breeder stage contributed most (59·8%) to λ, followed by non-breeder transition probabilities (34·2%) and a minor contribution of the fitness components of juvenile survival (6·0%).

FITNESS CONSEQUENCES OF NATAL ORIGIN

To estimate the fitness consequences associated with natal origin we combined all fitness components (juvenile and adult survival, recruitment probabilities, movement probabilities and reproduction) in one fitness measure (LRS). The expected LRS of a fledgling is given by $\mathrm{LRS} = \mathrm{S}^{\mathrm{J}} \times (\mathrm{T}^{\mathrm{HQ}} \times \mathrm{F}^{\mathrm{HQ}} + \mathrm{T}^{\mathrm{LQ}} \times \mathrm{F}^{\mathrm{LQ}})$ in number of fledglings produced. S^{J} is the survival until adulthood, T is the time an adult is expected to spend breeding in either HQ or LQ habitat and F is the annual fledgling production (counting only female offspring) in either HQ or LQ habitat.

Annual fledgling production was 2·5 times higher in HQ habitat ($\mathrm{F}^{\mathrm{HQ}} = 0{\cdot}160$) than in LQ habitat ($\mathrm{F}^{\mathrm{LQ}} = 0{\cdot}065$), averaged over 1985–96. Natal origin did not affect fledgling production of birds breeding in either HQ or LQ habitat (both analyses GLM, effect natal origin: $P > 0{\cdot}4$; $n = 205$ breeding attempts; year and individual entered as random effects). Using transition and survival probabilities (Fig. 2), we estimated life expectancy from adulthood and how many years a bird would spend breeding in HQ (T^{HQ}) and LQ habitat (T^{LQ}). Individuals from LQ natal origin had a 38% shorter reproductive life span (Table 1). Consequently, the expected LRS was 2·2 times higher for fledglings of HQ natal origin compared to fledglings of LQ natal origin (Table 1). Adults of LQ natal origin spent 34% of their breeding life span in HQ habitat (1·4 of 4·1 years) and consequently produced 56% of their LRS in HQ habitat. This implies that recruitment in LQ habitat as a stepping stone to HQ habitat is an important route for individuals of LQ natal origin, because we recorded only one individual of LQ natal origin ever to recruit directly into HQ habitat. Individuals of HQ natal origin spent 42% of their breeding life span in HQ habitat (2·8 of 6·7 years) and consequently produced 64% of their LRS in HQ habitat.

As mentioned previously, the low adult non-breeder survival of individuals of LQ natal origin could (in part) reflect permanent adult emigration. Therefore, we also calculated LRS assuming that the 4·4% mortality difference between non-breeders from LQ and HQ natal origin (LQ: 12·2% HQ: 7·8%; Fig. 2) was due entirely to a higher frequency of emigration to the non-breeder state in another population. In the emigration scenario total life span for juveniles that survived until adulthood did not differ, but reproductive life span is still 0·9 years shorter for individuals from LQ natal origin, due to less time spent as a HQ habitat breeder (Table 1). Consequently, the expected LRS was 1·6 times higher for fledglings of HQ natal origin than for fledglings of LQ natal origin (Table 1). In both scenarios LRS was smaller than 1, indicating that both LQ and HQ habitat are 'sinks'.

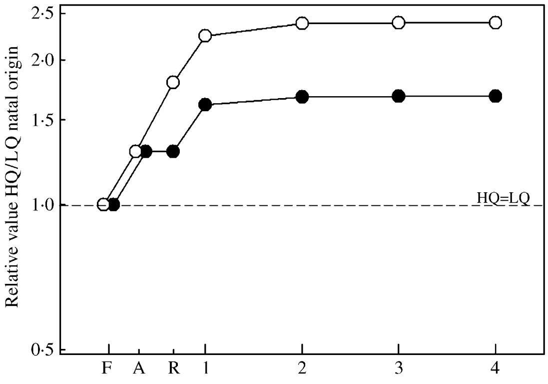

Fig. 3. Relative output of one fledgling from high-quality (HQ) natal origin compared to the output of one fledgling from low-quality (LQ) natal origin, in terms of the number of fledglings (F) that survive until adulthood (A), individuals that recruit in the breeding population (R) and fledglings produced after one, two, three and four generations. Open circles are values based on estimates in Fig. 2, closed circles are based on the 'emigration scenario' (see text). Note the logarithmic *y*-axis.

The fitness consequences of natal origin will still be underestimated slightly when fitness is calculated over one generation, because fledglings from HQ habitat are more likely to settle in HQ habitat themselves. Individuals of HQ natal origin produced 64% of their own offspring in HQ habitat, while 56% of the offspring of individuals of LQ natal origin will be of HQ natal origin. Assuming that survival, transition probabilities and reproductive output are constant in time, the differences in LRS can be extrapolated to many generations. After a few generations the difference in the expected number of future offspring between HQ and LQ natal origin levelled off to a 2·4-fold difference (Fig. 3).

Although counting the number of offspring alive at some moment in the future allows a comparison between measuring short- and long-term fitness consequences, it does not take into account at what point in life reproduction takes place. As this population was declining, offspring born later in life contribute more to λ than offspring born early in life. Because breeding life span is longer for offspring from HQ natal origin and age of first reproduction is independent of natal origin, we would expect that LRS underestimates the fitness benefits of HQ natal origin. The RV of a fledgling of HQ natal origin was 3·1 times higher than the RV of fledglings of LQ natal origin (calculated from model 2, Appendix S1), substantially higher than the 2·4-fold differences in LRS in number of fledged grand-offspring.

NATAL PHILOPATRY

If individuals settled very close to their natal site, this alone might explain the association between natal origin and breeding habitat quality. On the scale of the island individuals were highly philopatric, as virtually all individuals returned to the study area. However, within the study area, both sexes did not aggregate near or avoid their natal site compared to a randomly generated settlement pattern (randomization test, $n = 59$, $P > 0{\cdot}3$). The local natal dispersal distance was on average 444 m, much larger than the small distance between HQ and LQ habitat (< 100 m). Natal dispersal distance was not affected by natal origin (HQ: 441 ± 54 m, LQ: 449 ± 95 m, $F_{1,59} = 0{\cdot}04$, $P = 0{\cdot}83$) or sex (♂: 458 ± 61 m, ♀: 402 ± 37 m, $F_{1,59} = 0{\cdot}27$, $P = 0{\cdot}61$).

Discussion

SHORT- AND LONG-TERM FITNESS CONSEQUENCES

The fitness prospects of oystercatcher offspring were associated strongly with their natal origin during all life-stages, culminating in a 3·1-fold difference in RV between fledglings from HQ and LQ territories. Early in life, fledglings of HQ natal origin had a higher juvenile survival and later in life a higher adult survival as a non-breeder and a much higher recruitment probability to HQ habitat than individuals of LQ natal origin. Fledglings from LQ territories compensated some of their disadvantage by having a higher probability of promoting from LQ to HQ habitat once they had settled as breeder, although this result was based on few individuals. Because individuals recruited predominantly in the same type of habitat in which they were born, there was a positive correlation between natal origin of parents and their offspring. Consequently, effects of early conditions showed carry-over effects to future generations.

Effects of early conditions on fitness components occurred over a very long period and showed mostly positive, but also one negative effect, underlining the importance of integrating all fitness components into one fitness measure. Fitness consequences of natal origin became stronger as birds were followed over more life history stages (Fig. 3). Consequently, the quantification and interpretation of fitness differences between offspring of HQ and LQ natal origin in our study depends on whether only fitness components early in life, fitness components late in life, a fitness measure over a lifetime or a fitness measure over several generations is used.

Many studies have shown that early life fitness components are associated with differences in early conditions (see Introduction). Some studies measured all the fitness components necessary to calculate a lifetime fitness measure (Rose, Clutton-Brock & Guinness 1998; Kruuk *et al.* 1999; Visser & Verboven 1999; Reid *et al.* 2003), but did not quantify the relative contribution of short- and long-term consequences to fitness. Our study shows that long-term effects of rearing conditions can be at least as strong as short-term effects (compare slopes between life-stages in Fig. 3). Sensitivity analysis showed further that fitness components late in life had by far the strongest fitness effects in our population. Consequently, natural selection should favour rearing conditions that result in beneficial long-term effects more strongly than rearing conditions that favour short-term effects. The sensitivity pattern in oystercatchers seems opposite to the many studies that show that sensitivities of survival and reproduction are highest for youngest age-classes (Charlesworth 1980; Caswell 2001). However, in contrast to studies using age-structured population models, we aggregated adult fitness components over many age-classes and consequently their sensitivities were high. As such, we assumed implicitly that the long-term consequences of early conditions convey advantages in many more years than a similar effect on juvenile survival. We think this assumption is plausible because adult survival may depend, for example, on permanent aspects of phenotypic quality such as body morphology. Potentially, environmental stochasticity experienced during a life could reduce the strength of natural selection acting on the long-term effects of early conditions by distorting the strength of the correlation between offspring quality and individual quality later in life. Nevertheless, this study shows that early conditions may affect life-history decisions that take place up to 10 years later. Possibly, developmental pathways to important fitness components are selected for low susceptibility to environmental stochasticity as part of a bet-hedging strategy to reduce variance in fitness (Pfister 1998; Sæther & Bakke 2000; Reid *et al.* 2003). Important long-term effects of early conditions may therefore be a characteristic of many long-lived species, but more studies are required to evaluate this.

POTENTIAL PROBLEMS IN ANALYSING LONG-TERM EFFECTS

Because following individuals over an entire lifetime takes many years, partially incomplete life-histories were used. Right-censoring, in which not all individuals were followed until the end of their lives, could potentially bias estimates on the long-term effects of rearing condition. First of all, because few individuals lived to become a breeder and not all individuals were followed towards the end of their breeding career, estimates of breeder survival and transition probabilities were less reliable than those of non-breeders or juveniles. However, we have no reason to assume that reliability differed with respect to natal origin. Secondly, right-censoring might bias estimates of long-term effects because life-history traits might be age-dependent, and observations were biased towards young ages. However, adult survival is probably age-independent in this species (Schnakenwinkel 1970; Safriel *et al.* 1984), and recruitment probabilities are lower only for 3- or 4-year-olds (Bruinzeel 2004). Reproduction is strongly age-dependent, but did not differ with respect to natal origin. Therefore, biased sampling of young individuals is unlikely to have affected our main conclusions.

Finally, when averaging over all individuals with the same natal origin (cross-sectional comparison), we cannot disentangle whether short- and long-term effects of natal origin reflect accurately within-individual changes or that fitness components also varied due to the selective disappearance of certain quality individuals. To address this question we will have to wait until mark–recapture analyses can account for covariances between phenotypic quality and survival propensity (as in Cam *et al.* 2002; Pettifor *et al.* 2006).

HERITABILITY OF EARLY CONDITIONS

To our knowledge this is the first study that quantified the effects of early conditions on fitness over more than one generation, but results from other studies have hinted at the existence of similar effects by demonstrating a positive correlation between natal and breeding habitat quality (e.g. Verhulst *et al*. 1997) or between the quality of one's parents and one's own parental quality (e.g. Albon *et al*. 1983; Larsson & Forslund 1992). In such cases, early conditions (i.e. natal origin in this study) can be viewed as an inherited trait with a strong social component (Larsson & Forslund 1992). Differences between offspring of HQ and LQ natal origin could also have a genetic basis, although no genetic differentiation was found using eight polymorphic microsatellite loci (van Treuren *et al*. 1999) and the large gene flow might counteract any genetic differentiation.

NATAL ORIGIN AND OFFSPRING QUALITY

The effect of natal origin on fitness indicates that rearing conditions affected fledgling quality, which in turn mediated the fitness consequences. Fledglings of HQ natal origin were 10% heavier than fledglings of LQ natal origin (body mass corrected for size; $F_{1,294} = 11{\cdot}47$, $P = 0{\cdot}001$), and offspring mass is correlated positively with fitness in many species (e.g. Tinbergen & Boerlijst 1990; Magrath 1991; Green & Cockburn 2001; Perrins & McCleery 2001). Thus fledging mass constitutes a promising candidate for further investigation. Body size and date of birth are less likely candidates, as neither body size (PC1 of three structural size parameters; $F_{1,294} = 1{\cdot}03$, $P = 0{\cdot}31$) nor date of birth ($F_{1,294} = 2{\cdot}39$, $P = 0{\cdot}12$) depended on natal origin.

NATAL PHILOPATRY AND DISPERSAL

Dispersal at a scale larger than the study site remains a problem for estimating fitness consequences in the wild. In the majority of studies, only local re-sightings of individuals that returned to the study area are available (Bennets *et al*. 2001). Consequently, effects of early conditions on apparent local survival or recruitment are confounded by possible similar effects of early conditions on dispersal behaviour. The oystercatcher is a relatively good study species to account for dispersal, as information from the study area (99% locally re-sighted) can be compared with information from a larger scale (24% dead recovered).

Juvenile oystercatchers leave the study area after fledging, but practically all birds that survived until adulthood returned, and as such juvenile oystercatchers, were extremely philopatric (Martin & Hannon 1987). More males than females returned to their natal area at adulthood, which was due probably to differences in survival rather than philopatry. The cause of this sex difference is not clear, although there is a small sexual dimorphism in bill morphology and associated feeding specialization that may have played a role (Durell *et al*. 2001). Effects of early conditions did not differ between the sexes in the adult phase, as expected for species with minor sexual dimorphism and comparable sex roles in breeding (Kruuk *et al*. 1999; Lindström 1999).

Although juveniles did not disperse permanently, some adult non-breeders did leave the study area subsequently before acquiring a territory (van de Pol, unpublished). However, our finding that natal origin was strongly associated with fitness was robust to specific assumptions about permanent adult emigration. When we assumed that the low non-breeder survival of individuals of LQ natal origin was caused by permanent adult emigration, large fitness differences remained (Fig. 3).

IMPLICATIONS FOR LIFE HISTORY DECISIONS AND POPULATION DYNAMICS

Our results have implications for many oystercatcher life history decisions, but here we will focus on the life history decisions of where and when to settle. Ens *et al*. (1995) developed a settlement model to explain why some individuals accept territories in LQ habitat, given the large difference in reproductive success with HQ territories. This model hypothesized that non-breeders selecting a breeding habitat could attain higher fitness by waiting for a few years ('queue') until a HQ habitat becomes available, instead of settling immediately in LQ habitat for which competition is low. Their 'queue model' calculates the frequency dependent evolutionary stable settlement strategy, using the expected LRS (in fledglings) as a fitness currency. There were insufficient data to investigate the fitness consequences of natal origin beyond fledging when the model was developed, and Ens *et al*. (1995) therefore assumed that fledgling fitness prospects were independent of natal origin. However, with more data available we can refute the assumption that fledglings from HQ and LQ contribute equally to fitness. Incorporating higher fitness prospects of offspring born in HQ habitat in the queue model should shift the equilibrium to more non-breeders opting for HQ habitat that are also willing to wait for longer, instead of settling immediately in LQ habitat. Furthermore, our results show that individuals of different natal origin have different settlement patterns, with fledglings from LQ territories having a much lower probability of settling in HQ habitat than fledglings from HQ territories. The queue model by Ens *et al*. (1995) is not sufficiently detailed to explain why these different settlement strategies exist; this would require the incorporation of condition-dependent settlement strategies.

Finally, this study shows that using short-term or incomplete fitness estimates can lead to incorrect inferences when quantifying source–sink population interactions. Breeders in HQ habitat produced annually 2·5 times more fledglings than breeders in LQ habitat. However, not all fledglings were of the same quality. Consequently, breeders in HQ habitat each year contributed 7·8 times (2·5-fold difference in quantity of fledglings

× 3·1-fold difference in RV of one fledgling) more to λ than breeders in LQ habitat. As such, breeders in LQ habitat contributed only marginally to the growth rate of this population of oystercatchers.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://www.blackwell-synergy.com

Appendix S1. The structure of the population matrix models.