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Natal dispersal in the western gull: proximal factors and fitness consequences

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Summary

1. Natal dispersal distance (NDD; the distance between natal site and recruitment site) was studied in relation to proximal factors including sex, cohort, recruitment age, nesting density, nest site quality; and also within-colony movements of prospecting prebreeders among 133 recruits of two cohorts (1979–80) in a large, dense colony of western gulls *Larus occidentalis* (Audubon) on South-east Farallon Island, California. NDD was also studied in relation to ultimate factors, assessed from total number of chicks fledged to 1994, survival of breeding adults, and fitness-related life history traits, including brood size and hatching date. The Farallones colony is an unusual case in that it includes 50% of the species population and 90% of all western gulls breeding within a radius of 1000 km. Hence, potential recruits could choose between locations within the Farallones colony, but had limited choice to recruit at other colonies.

2. Among prebreeders, distance from natal site to prospecting site increased with age among gulls aged 2 to 4 years, and stabilized in 4- to 8-year-olds. Most 2-year-olds prospected on their natal sites.

3. Compared to other bird species, natal philopatry was strongly developed in both sexes, but was significantly greater in males (median distance between natal and recruitment site among males, 17 m; median distance among females, 50 m).

4. More philopatric males nested in areas of higher density and with a tendency for more nest cover ($P = 0{\cdot}080$, when controlling for the effect of density). A non-linear relation between NDD and recruitment age among males resulted from shorter NDD in 4-, 5- and 6-year-olds compared to 3-year-olds and males older than 6 years. There was no relation between NDD and recruitment age in females.

5. Males who had hatched early in the season (individuals who were, on average, more dominant, with higher prebreeder survival and recruitment probability; Spear & Nur 1994) had shorter NDD than males who hatched later.

6. Fitness costs associated with natal philopatry were detected in both sexes. More philopatric males survived significantly less well than did less philopatric males. Average number of chicks fledged among experienced females (6–11 years breeding experience) was significantly lower among more philopatric compared to less philopatric individuals, as was cumulative number of chicks fledged for all females (as of 1994).

7. Thus, whilst philopatry was well developed in these gulls, the trait appeared maladaptive. This paradoxical result may be related to an extended period of poor food supply (1989–94) in the Gulf of the Farallones. We hypothesize that fitness costs associated with philopatry reflect different life history strategies where high philopatry may be part of a high effort strategy characterized by higher reproductive effort and lower survival. These results are consistent with the view that relative advantages and disadvantages between life history strategies could lead to selective equilibrium, depending on environmental conditions.

Key-words: *Larus occidentalis*, natal philopatry, natural selection, prebreeding behaviour, recruitment.

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Introduction

In birds, movement from the natal site to the recruitment site (natal dispersal) usually accounts for most dispersal in the life of an individual; in general, little relocation occurs after the first breeding attempt (reviewed in Greenwood & Harvey 1982). Thus, detailed insights regarding broader issues such as life-history patterns and population regulation can be gained through studies of natal dispersal (reviewed in Baker 1978; Greenwood & Harvey 1982; Shields 1982; Johnson & Gaines 1990; Part 1991). Natal philopatry (breeding in the vicinity of the natal site) is thought to be adaptive because individuals benefit from local experience with resources, predators, and conspecifics, as well as from enhanced competitive ability resulting from increased 'self-confidence' on familiar grounds (references above; and see Oring & Lank 1984). Greenwood, Harvey & Perrins (1979a) suggested that related individuals nesting adjacent to one another might experience increased productivity because of reduced aggression via kin selection.

In philopatric species, greater natal dispersal in one sex compared to the other might be adaptive to avoid inbreeding (Greenwood, Harvey & Perrins 1979b; Shields 1982; Oring & Lank 1984; Pusey 1987; Johnson & Gaines 1990; but see Moore & Ali 1984). A higher incidence of natal philopatry in male birds, compared to females, could also result from mating systems in which the male's main role is usually to obtain and defend the breeding territory and to feed the female and young (Greenwood 1980; for exceptions see Dow & Fredga 1983; Oring & Lank 1984). Thus, males more than females, would benefit from local experience.

The authors are not aware of studies that have quantitatively examined the relationship of natal dispersal distance (NDD) with quality of nesting habitat, and at the same time with fitness components (breeding performance and survival rate). A problem encountered is the difficulty of assessing quality of nesting habitat directly on the basis of environmental features. Indeed, most studies have used breeding performance itself as the measure of habitat quality, thus confounding the relationship between NDD and habitat quality with that of NDD and fitness. Other problems in studies of how NDD might relate to habitat quality and fitness of the individual are under-representation of unsuccessful breeders and emigration from the study area. Yet another potential problem for many species is that the nesting territory functions both as a feeding area and nesting site. Hence, both food supply and the availability of favourable nesting habitat can affect nesting habitat quality.

NDD was examined in two cohorts of western gulls [*Larus occidentalis* (Audubon)] ringed as chicks on South-east Farallon Island, California, in 1979 and 1980. Birds breeding for the first time, or who were alive but did not recruit, were monitored each year from 1982 to 1994. Due to a low emigration rate (see Methods), it is believed that the present study was able to monitor NDD of >95% of the birds who reached adulthood. The study had two main objectives. First, to identify proximal factors affecting NDD, it examined prospecting behaviour of pre-breeders and effects of sex, cohort, recruitment age, nesting density, and nest site quality on NDD. Second, to identify possible fitness consequences, it examined the relationship of NDD to fitness components, assessed from annual breeding performance, total number of chicks fledged to 1994, survival of breeding adults, and life history traits affecting survival of pre-breeders and recruitment probability (brood size, hatching date; Spear & Nur 1994; Spear, Sydeman & Pyle 1995). Thus, in the second section of this paper ultimate factors are examined that may influence the evolution of NDD. In the final section possible benefit from nesting adjacent to relatives is examined.

Methods

STUDY POPULATION

During 1979–94, about 25 000 western gulls bred annually on South-east Farallon Island (Ainley *et al.* 1994). The population is stable or declining slightly and its nesting distribution covers nearly all of the 44 ha island. The range and breeding distribution of the nominate race of western gull (which includes the Farallones colony) is entirely restricted to coastal Washington, Oregon, and California (Spear 1988), and nearly all colonies are accessible for examination for presence of ringed individuals. A large ringing operation (≈1000–2000 chicks ringed per year) has been underway on SE Farallon Island since 1971. As a result, about one in 13 adult Farallon gulls were ringed during this study. Results of extensive searching for ringed Farallon western gulls breeding in other colonies within the range of this race indicated that the emigration rate from SE Farallon Island was very low during the 1970s and 1980s (Spear & Nur 1994; Spear *et al.* 1995), and has apparently remained low. Observations made in 1995 at an expanding colony on Alcatraz Island, only 45 km from SE Farallon Island and the nearest major colony, revealed that among 200 western gulls breeding there which were examined for rings, only one bird had been ringed on SE Farallon Island (M.E. Brown, personal communication).

One would expect a low rate of emigration from SE Farallon Island simply because there are only three islands within a 500 km radius of the Farallones that are suitable for gull colonies (Carter *et al.* 1992). For the 1000 km section of coastal California so defined, 90% of the breeding western gull population is found on the Farallon Islands; in contrast, the only other colonies of moderate size composed about 7% of the breeding population. The remaining 3% breed at additional scattered locations along the coast.

MONITORING MOVEMENT OF PREBREEDERS AT THE COLONY AND NATAL DISPERSAL DISTANCE

Pairs of western gulls hatch up to three semiprecocial young. In 1979 and 1980, hatching date and brood size at hatching were recorded for 832 chicks (446 chicks in 1979, and 386 in 1980; see Spear & Nur 1994). Each nest site was mapped and those not easily relocated were marked with a metal stake. All chicks were ringed once on each leg with combinations of Warner darvic colour rings, Lambournes incoloy rings and US Fish & Wildlife Service stainless-steel rings.

Throughout the breeding season of each year 1982–92, the colony was searched daily for ringed birds who were prospecting for territories, or who were occupying territories for the first time (details in Spear *et al.* 1995). A paired gull had 'recruited' once it or its mate produced an egg. It is believed that few, if any, recruits were missed as a result of egg loss because in only two cases did a pair of apparent recruits maintain a nest yet fail to produce an egg. Movement onto the Farallones by birds hatched on the Farallones, but who had first bred elsewhere, was not considered a problem because of scarcity of alternative breeding sites (see above), nor was within-colony movement a problem because Farallon gulls rarely move to new nesting locations more than 10 m distant from the previous site (Pyle *et al.* 1991); maximum observed = 29 m, $n = 1129$.

From the original sample of 832 chicks 133 recruits were recorded; of these, the recruitment age for 131 was known. None were paired with one another. Each recruit was sexed visually by comparing its size to that of its mate (Pierotti 1981; Spear 1988). The distance was measured directly (to 1 m) between the recruitment nest site and the natal nest site of each recruit; following Greenwood (1980) NDD was thus defined. The maximum possible NDD within the study area, including the adjoining island, West End, was 1400 m on the east–west axis and up to 600 m on the north–south axis.

To gain insight into the dynamics of recruitment as related to NDD, movements were also recorded within the colony of ringed prebreeders who were prospecting for territories in 1981–92. A subsample of 44 individuals who were seen during at least 2 years prior to recruitment was studied to examine changes in prospecting behaviour with age. Some were seen in multiple years and, in all, 96 sightings were made of these birds. This value does not include multiple sightings in the same year; in these cases mean distances were analysed for each year of observation. Sightings at 'club sites' (Tinbergen 1953) where prebreeders gathered when not prospecting in the colony proper were excluded. Distances from prospecting sites to natal were compared with respect to age.

Ring loss rates indicated that fewer than 0·5% of the studied population would have lost both rings and become unrecognizable (Spear *et al.* 1995).

MONITORING FITNESS COMPONENTS

Five factors were examined that were considered indicators of fitness. These included: (i) hatching dates of recruits; and (ii) brood size from which they originated. These factors were considered as fitness indicators because western gulls which hatch early in the season, and into large broods, survive best during the postfledging period (Spear & Nur 1994). The study also considered: (iii) survival, to 1994, of 114 birds who recruited; (iv) average number of young fledged per breeding attempt (range: 0–3 fledglings); and (v) cumulative number of young fledged, from 1982 to 1994, for 98 members of the sample group. Cumulative numbers of young fledged were examined as an index of fitness that reflects both survival and annual reproductive rate and their possible interaction.

The reproductive success of the 98 gulls who recruited inside study plots was monitored (35 of the 133 recruits nested outside the plots). Owing to logistic difficulty, it was not possible to monitor reproduction for 15·1% of the breeding attempts by the 98 gulls (87 of 577 'gull-years'); 30 individuals were not monitored in 1 year that they had bred, and 25 were not monitored in 2 or more years. An adjustment was made for years of missing data in regression models on these data, where appropriate (see below). None of the gulls monitored for reproductive success skipped a year of breeding subsequent to recruitment.

MONITORING OF HABITAT QUALITY AND DENSITY AT THE NEST SITE

With few exceptions, western gull chicks stay within 1 m of the nest in their first 7 days of life (LBS, PP, personal observation). Predation by conspecifics on eggs and chicks, and exposure, are major mortality factors (Spear *et al.* 1987; Penniman *et al.* 1990). Nests are placed at a location offering the most protection (see Montevecchi 1978; Pierotti 1982); that is, 'cover,' in the form of rocks, wood and debris projecting above the level of the nest, or above crevices or burrows used as hiding places by small young. Analysis of young fledged per pair indicated a significant positive relationship with nest cover. The nesting territory does not serve as a significant foraging area for western gulls breeding on SE Farallon Island (LBS, PP, personal observation). Therefore, it was possible to quantify nesting habitat quality by measuring the amount of available nest cover on each territory (defined below).

From direct observation, and to avoid interobserver difference, a single individual (Pyle) monitored nest cover. This was undertaken in early June each year.

Nest cover was estimated as the proportion of area within 1 m of the nest composed of objects or crevices projecting 15 cm or more above or below the nest level. Vegetation was trampled by the gulls early in each breeding season and was not considered as cover. To compare nesting habitat quality between the natal and recruitment site, cover was recorded at respective sites for 128 gulls of the sample group. In all, nest cover was recorded at nest sites of 90 gulls of known NDD in 266 gull-years where number of young fledged was also monitored (see above).

During observations on nest cover, distance to nearest neighbour's nest was also measured, which is considered in the present study as an inverse measure of nesting density.

DOES NESTING ADJACENT TO A RELATIVE AFFECT REPRODUCTIVE SUCCESS?

Many males nested adjacent to their (ringed) fathers, and because of this it was of interest to examine the possible effect on an individual's productivity of having a living relative nest nearby (see Greenwood *et al.* 1979a). Two brothers also nested adjacent to one another. Breeding performance of sons nesting adjacent to their fathers was compared with gulls nesting adjacent to their natal territory but whose fathers were dead; the two brothers nesting adjacent to each other were included in the former group. Breeding performance was monitored for 17 adjacent sons/brothers, and averaged for each gull for which more than 1 year was monitored. Seven males nested adjacent to a living father/brother, with 15 monitored breeding attempts, and 10 sons nested adjacent to their dead father's territories, making 19 breeding attempts. These gulls had 0–3 years breeding experience.

STATISTICAL ANALYSES

Following *STATA* (Stata Corporation 1997), simple and multiple regression was used to model dependent variables for which outcomes were continuous. To analyse survivorship in relation to covariates the Cox Proportional Hazards Model was used (Cox & Oakes 1984; Stata Corporation 1997). Results of the present study are presented in terms of the hazard rate function (Cox & Oakes 1984), which is proportional to the force of mortality, and inversely related to survival.

For regression analyses, logarithmic transformation was used to normalize dependent variables. Regression analyses were only used where residuals (with variables transformed as necessary) met assumptions for approximation to normality (Skewness/Kurtosis Test for Normality of Residuals, $P > 0{\cdot}05$, Stata Corporation 1997). The assumption of homoscedasticity of residuals was examined by testing residuals using the Cook–Weisberg test, as described by the Stata Corporation (1997); in no analyses presented here was there significant heteroscedasticity (all $P > 0{\cdot}1$). Distance to the nearest neighbour and NDD (when analysed as an independent term) were also log-transformed; the effect was to linearize the relationship of these variables to dependent terms. Although analyses in the present study violated the assumption of regression analysis that independent variables are measured without error, Seber (1977, pp. 155–162) points out that error in the independent variable leads to bias in estimating regression coefficients, but otherwise has little effect on statistical properties of the *F*-test (*P*-values). Because some terms requiring log-transformation included values of zero (NDD and prospecting distance), transformations were calculated as the log (distance + 1). Experimentation with different modifications (e.g., log – distance + 0·5) demonstrated no appreciable effect of choice of modifications on quantitative outcomes of respective analyses. Where residuals could not be normalized, the Mann–Whitney *U*-test was used.

Two methods were used to test for non-linearity in the relationship of NDD to covariates: first by testing for the significance of quadratic terms, and second by testing for non-linearity given replicated observations, as described by Zar (1996, p. 338). Where quadratic terms were significant, cubic terms were examined; where cubic terms were significant (one such case), the significance of quartic terms was examined. For the test of deviation from quadraticity and/or cubicity the same method was used as described by Zar (1996, p. 338) for departure from linearity.

Only significant terms ($P < 0{\cdot}05$) were included in the final model, except where linear main effects were required because of inclusion of higher order effects. Separate analyses were run on each sex if there was significant interaction between sex and a relevant independent variable, or if preliminary analyses showed a significant effect of a given term on one sex, but not the other. Note that terms 'sex,' 'cohort,' and ' year' are categorical. The term 'ring number', treated as categorical, was included where individuals were observed multiply in different years; that is, in models examining prospecting distance of prebreeders from the natal site in the colony, and number of chicks fledged in relation to breeding experience. The purpose was to test and control for an individual main effect; that is, we tested whether multiple observations for a single bird showed correlated response, and controlled for this accordingly.

Preliminary analyses demonstrated a highly significant correlation between the terms 'years of age' and 'years of breeding experience', among gulls monitored for breeding performance ($r = 0{\cdot}873$, d.f. = 422, $P < 0{\cdot}0001$; see also Pyle *et al.* 1991). Experience had the stronger effect on breeding performance when both terms were included in the same model. Therefore, to avoid colinearity between the two terms, age was dropped from these analyses.

Results

BEHAVIOUR OF PROSPECTORS

Forty-four individuals were seen prospecting on SE Farallon Island at least 2 years before they recruited. These prospectors were seen in the colony proper or loafing at Farallon club sites in 94% of the intervening years (at least 1 year after first being seen and before recruitment), indicating that most attended the colony at least part of the time each year.

Distance from the natal site to the site at which western gulls prospected (log-transformed) did not differ with sex but varied significantly among individuals, and, for a given individual, increased significantly with age (Table 1). In this analysis we used an ANCOVA-type model (for each individual, all sets of interyear sightings were fit with the same slope, but each individual was allowed to have a different intercept; see below for details of whether slopes differed among individuals). The effect of age on prospecting distance was non-linear (Table 1, Fig. 1): there was a substantial increase in prospecting distance from age 2 years to age 3 years, followed by a plateau thereafter. Once between-individual variation was statistically accounted for, the within-individual trajectory showed significant deviation from linearity and from quadraticity (Table 1). A cubic polynomial relationship, with three terms, accounted for 13·8% of the variation in prospecting distance (partial $r^2 = 0{\cdot}138$); that of the linear, quadratic, and cubic terms accounted for 5·0%, 4·1% and 4·7%, respectively. There was no deviation from cubicity.

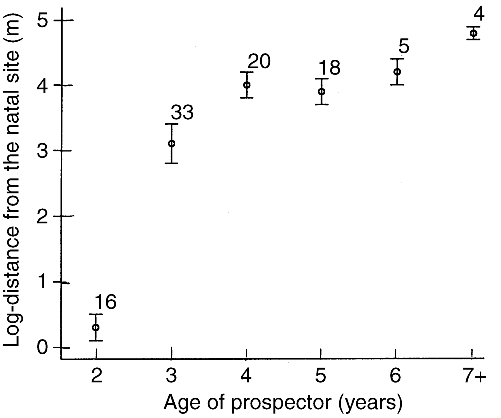

Fig. 1. Log-distance from the natal site to the prospecting site, as related to age among western gulls seen prospecting in the colony during at least 2 years prior to the year of recruitment. For graphic simplicity, this figure pools age-related variation in prospecting distance across individuals, whereas analyses presented in Table 1 partition age-related variation in prospecting distance into between-individual and within-individual effects. Shown are the means (circles) ±1 SE (vertical bars) above and below the mean. Numbers above bars are sample sizes.

Two-year-olds usually prospected at their natal site (12 of 16), 3-year-olds only rarely (<10%), and prospectors more than 3 years old were not seen prospecting at their natal site. We examined whether or not the linear trend for prospecting distance to increase with an individual's age differed among individuals. The interaction between age (linear term) and individual was not significant (Table 1). This result indicated that the effect of age on prospecting distance was similar among individuals, however, the power to detect a significant interaction was weak because the denominator included only 6 d.f. when carrying out that test.

Table 1. Multiple regression model for distance between prospecting site and natal site (=dependent term; log-transformed) of prebreeders in the SE Farallon Island colony as related to age (at the time observed prospecting) and sex. The model includes the categorical term 'individual' (ring number). All individuals ($n = 44$) were seen prospecting in the colony during at least 2 years before the year that they recruited. The 'adjusted for' column refers to terms included in the model (main effects) when assessing the effect of a primary term. F-values refer to including the term in the full model in the case of those having a significant effect, and adding the term to the full model in the case of rejected terms. The 'linear age' term refers to a linear model with no higher order terms present; 'quadratic age' refers to a model including only the linear and quadratic terms. Terms with more than one component, separated by •, indicate interactions between component terms; d.f. refers to numerator d.f. in F-test

Primary term	Adjusted for	d.f.	Coefficient	SE	F-value	P-value	Partial R^2 × 100
Model $F_{46,49} = 5{\cdot}49$, 83·8% of variance explained							
Age	Individual						
linear		1	0·466	0·1460	10·19	0·0020	5·0
quadratic		1	−0·174	0·0559	9·63	0·0030	4·1
cubic		1	0·101	0·0271	14·14	0·0005	4·7
Individual	Age	43	–	–	1·87	0·0170	70·0
Rejected terms							
Sex	Individual, age	1	0·856	0·9800	0·76	0·4000	–
Age (linear term) • Individual	Individual, age	43	–	–	2·07	0·1800	–

NATAL DISPERSAL DISTANCE, SEX, COHORT AND RECRUITMENT AGE

Among recruits, NDD of males was significantly less than that of females, with or without controlling statistically for recruitment age (males, median 17 m, range, 0–442 m; females, median 50 m, range, 2–321 m; Table 2, Fig. 2). These short dispersal distances compared to island dimensions (600 × 1400 m) indicate that NDD was generally not being constrained by the size of the island. Whereas 58% of the males dispersed <20 m, only 13% of the females dispersed <20 m. Only 3·3% of the females, but 22·2% of the males, had territories abutting or incorporating part or all of their natal territories.

Recruitment age and NDD were not significantly

Table 2. Linear regression models for natal dispersal distance (log-transformed) as related to sex, cohort, and recruitment age (RA). Distinct models are indicated by letters (a) to (i). The ‘adjusted for’ column refers to terms included in the model (main effects) when assessing the effect of a primary (independent) term. Terms with more than one component, separated by •, indicate interactions between component terms. Values for linear terms were calculated after quadratic and interaction terms were dropped from the model. All numerator d.f. = 1

Primary term	Adjusted for	Coefficient	SE	*F*-value	*P*-value	Sample *n*
Dependent term: Natal dispersal distance						
(a) Sex	–	−0·9080	0·2110	18·47	<0·001	133
(b) Cohort	Sex	0·0014	0·2120	0·00	1·000	133
(c) RA	Sex	0·0822	0·0783	1·10	0·300	131
(d) RA • Sex	–	–	–	1·43	0·230	131
(e) Males						
RA linear	–	0·2020	0·1430	2·00	0·160	71
(f) Males						
RA quadratic	–	0·1930	0·0762	6·44	0·013	71
(g) Males (excluding 3-year-olds)						
RA linear	–	0·3540	0·1770	4·00	0·049	66
(h) Males (excluding birds >7 years of age)						
RA linear	–	−0·2640	0·1870	1·99	0·160	65
(i) Females						
RA linear	–	0·0093	0·0821	0·01	0·900	60

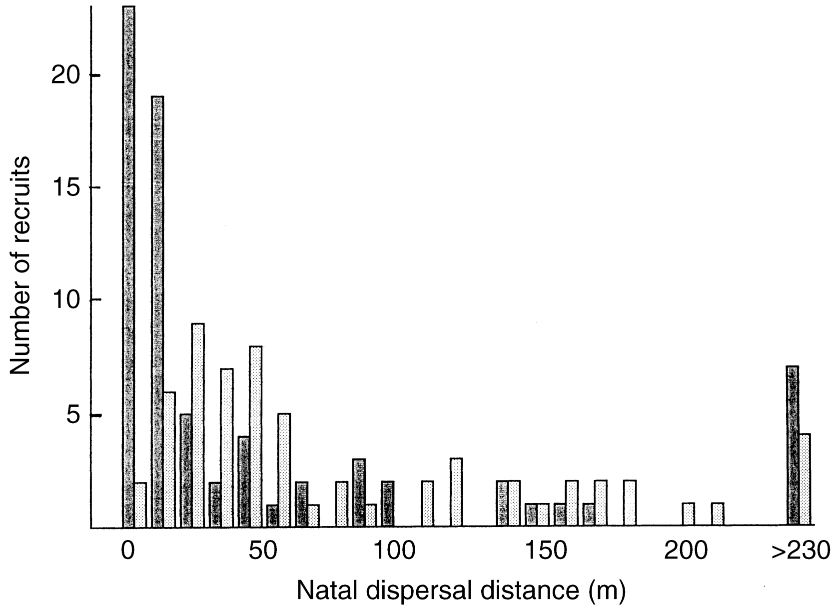

Fig. 2. Natal dispersal distance in male (dark bar) and female (light bar) western gulls recruiting on the SE Farallon Island. Total number of males and females was 72 and 61 birds, respectively.

related (controlling statistically for sex; Table 2c), however, separate analyses on each sex indicated a significant quadratic relationship in males, resulting from greater NDD of 3-year-olds and of males aged >7 years, compared to 4-, 5-, and 6-year-olds (Fig. 3). [We tested for significant deviation from lack-of-fit of the quadratic relationship and found none; $F_{2,68} = 3{\cdot}01$, $P > 0{\cdot}05$]. If 3-year-old males are excluded, the relation between age and NDD is significantly positive (Table 2g); if males >7 years are excluded the relation shows an insignificant, negative trend (Table 2h). NDD was very similar among the two cohorts (Table 2b). The relation between NDD and recruitment age was insignificant among females.

RELATIONSHIP BETWEEN NATAL DISPERSAL DISTANCE, NESTING DENSITY AND AMOUNT OF NEST COVER

NDD among males, but not females, increased significantly with increase in nearest-neighbour distance (NNB, an inverse measure of density) measured at the recruitment site (Table 3c & d, Fig. 4). Thus, nesting density was greater among male recruits having shorter NDD. For females the effect was in the same direction; the difference between the sexes in the effect of nearest-neighbour distance on NDD was not significant (Table 3b). NDD was not correlated with distance to the nearest neighbour's nest at the natal site (Table 3e).

There was a marginally insignificant ($P = 0{\cdot}051$) increase in amount of nest cover at the recruitment site with decrease in NDD among males (Table 3k). Thus, males who recruited closer to their natal sites tended to have more nest cover (better quality nesting habitat) compared to those recruiting farther away. The effects of either of the two terms included in the same model differed little from their respective effects, as indicated by the original models when the second term was not present (Table 3m). Hence, NDD was more closely associated with density at the recruitment site than it was with nest cover.

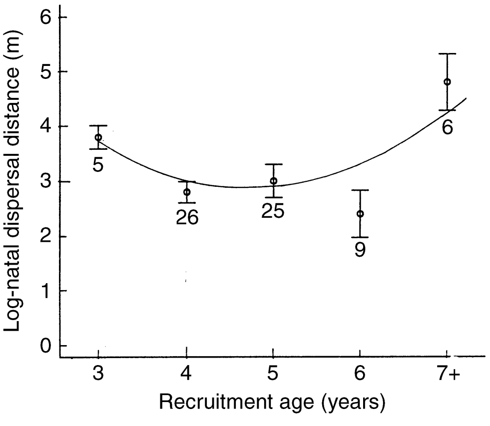

Fig. 3. Log-natal dispersal distance in relation to age of recruitment in male western gulls. Shown are the means (circles) ±1 SE (vertical bars) above and below the mean. Numbers below bars are sample sizes. Also shown is the line of best fit.

RELATIONSHIP OF NATAL DISPERSAL DISTANCE WITH FITNESS COMPONENTS

Hatching date of recruits, but not their natal brood size, was significantly related to NDD in males but not in females (Table 4, Fig. 5). Males that hatched earlier in the season had shorter NDD than males hatching later. The sex-specific difference in the effect of hatching date was significant (Table 4).

Survival probability during the period 1982–94 increased with *increase* in NDD in males (Table 5, Fig. 6), but not among females, although the trend was in the same direction for both sexes. The difference between the sexes with respect to the effect of NDD on survival was not significant.

However, NDD and nesting density were correlated ($r = 0{\cdot}272$, d.f. = 129, $P = 0{\cdot}002$). Therefore, to determine whether the relationship of NDD to survival was confounded by nesting density (measured as the distance to the nearest neighbour, NNB), we tested for a relationship between survival and NNB. The results indicated that the effect of nesting density on survival was not significant ($P = 0{\cdot}6$, Table 5); that is, that the observed relationship between NDD and survival probability was independent of the effect of nesting density.

To control for the effect of experience on reproductive success (see Pyle *et al.* 1991), we grouped breeding experience into one of three categories: inexperienced [0–2 years], moderately experienced [3–5 years], and experienced [6–11 years]. These experience groups are consistent with changes in reproductive success with experience as observed in other demographic studies (Pyle *et al.* 1997). There was no significant relation between number of chicks fledged per attempt and NDD within each experience group, with both sexes considered simultaneously (F-tests, while controlling for sex, all $P > 0{\cdot}1$; not shown). For inexperienced parents, the effects of NDD on number of chicks fledged were similar between the sexes, however (F-test for interaction, $P > 0{\cdot}6$); for the most experienced parents, the effects of NDD on number of chicks fledged showed a tendency to differ between the sexes ($P = 0{\cdot}055$), and in any case, the slopes were in opposite directions (Tables 6c and h).

Separate analyses on each sex indicated that, among experienced females, chicks fledged per attempt increased with increasing NDD (Table 6h, Fig. 7). There was little relation between NDD and fledging success in inexperienced or moderately experienced females, nor for any experience group among males.

Heterogeneity of slopes, the tendency for slopes relating chicks fledged with NDD to differ when compared among the three experience groups (a test with 2 d.f. in the numerator), was not significant among

Table 3. Linear regression models for natal dispersal distance (log-transformed) as related to distance to nearest neighbour (NNB, log-transformed) at the recruitment site, NNB at the natal site, and nest cover at recruitment site. Distinct models are indicated by letters (a) to (m). The 'adjusted for' column refers to terms included in the model (main effects) when assessing the effect of a primary term. Terms with more than one component, separated by •, indicate interactions between component terms. Values for linear, non-interaction terms were calculated after interaction terms were dropped from the model. All numerator d.f. = 1

Primary term	Adjusted for	Coefficient	SE	*F*-value	*P*-value	Sample *n*
Dependent term: Natal dispersal distance						
(a) NNB at recruitment site	Sex	0·8460	0·2220	14·50	<0·001	131
(b) NNB • Sex	–	–	–	3·17	0·078	131
(c) Males	–	1·1720	0·3010	15·19	<0·001	71
(d) Females	–	0·3750	0·3230	1·35	0·250	60
(e) NNB at natal site	Sex	−0·1000	0·3190	0·10	0·800	127
(f) NNB • Sex	–	–	–	0·06	0·800	127
(g) Males	–	−0·1800	0·4840	0·14	0·700	69
(h) Females	–	−0·0170	0·4090	0·00	0·900	58
(i) Cover at	Sex	−0·0146	0·00794	3·38	0·068	128
(j) Cover • Sex	–	–	–	1·18	0·300	128
(k) Males	–	−0·0213	0·0107	3·94	0·051	70
(l) Females	–	−0·0034	0·0118	0·08	0·800	58
Males						
(m) Cover	NNB	−0·0178	0·0101	3·15	0·080	70
(m) NNB	Cover	0·2300	0·0693	11·00	0·002	70

Table 4. Linear regression models for natal dispersal distance (log-transformed): effect of recruit's hatching date and brood size. Distinct models are indicated by letters (a) to (e). Models (a) and (e) included the term sex. Terms with more than one component, separated by •, indicate interactions between component terms. Tests for interactions included main effects. The interaction between sex and brood size was insignificant. Sample *n* was 133 birds, 72 males and 61 females. All numerator d.f. = 1

Primary term	Coefficient	SE	*F*-value	*P*-value
Dependent term: natal dispersal distance				
(a) Hatching date	0·0504	0·0281	6·69	0·011
(b) Hatching date • Sex	–	–	7·37	0·008
(c) Males	0·0962	0·0281	11·68	0·001
(d) Females	−0·0079	0·0246	0·10	0·700
(e) Brood size	−0·2380	0·1830	1·68	0·200

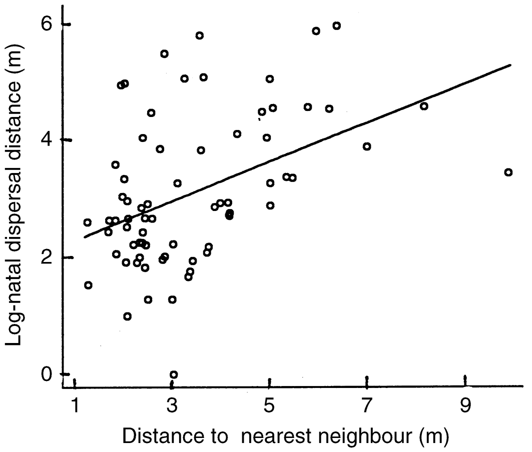

Fig. 4. Log-natal dispersal distance in male western gulls in relation to distance to nearest neighbour's nest at the recruitment site, including line of best fit.

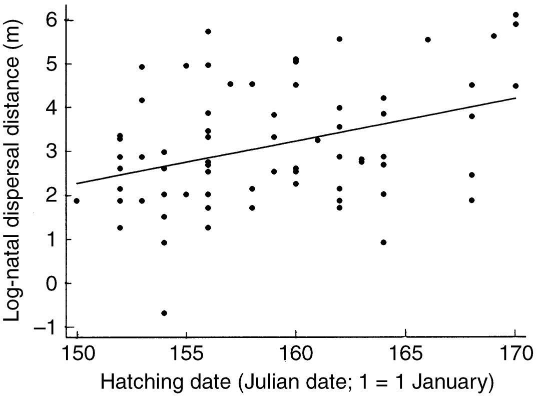

Fig. 5. Log-natal dispersal distance in relation to date of hatching of the recruit in male western gulls, including line of best fit. Date of hatching is shown as the Julian date (1 January is denoted by a value of 1, and 31 December as 365).

Table 5. Cox Proportional Hazards Model for relationship of mortality during 1982–94 with natal dispersal distance (NDD, log-transformed), and distance to nearest neighbour (NNB, log-transformed) in male and female western gulls. Shown are hazard rate regression coefficients and associated statistics. Effect of nearest-neighbour distance on survival was analysed while controlling for natal dispersal distance. Distinct models are indicated by letters (a) to (e). Terms with more than one component, separated by •, indicate interactions between component terms. Sample size was 61 males and 53 females. All d.f. = 1. *LRS* = likelihood ratio statistic. Recruitment age was not included because it was not correlated with NDD

Primary term	Coefficient	SE	*LRS*	*P*-value
(a) Males: NDD	−0·242	0·122	4·08	0·043
(b) Females: NDD	−0·026	0·168	0·02	0·800
Test of interaction:				
(c) Sex • NDD	–	–	1·60	0·200
(d) Males: NNB	−0·235	0·493	0·23	0·600
(e) Females: NNB	−0·336	0·575	0·35	0·600

Table 6. Linear regression models for relationship between number of young fledged per breeding attempt (the dependent term), natal dispersal distance (NDD, log-transformed), years of breeding experience, and sex. Years of breeding experience were stratified into three categories. Each individual was included once per experience group and reproductive success was averaged for each individual in each experience group. Regressions were weighted by square root of number of monitored breeding attempts per individual (see text). Distinct models are indicated by letters (a) to (j). Slope 'trend' refers to tendency for slope to increase or decrease as experience category increases. Sample *n* was 57 males and 41 females

Primary term	Coefficient	SE	*F*-value	*P*-value	*n*	Numerator d.f.
Males						
(a) Experience = 0–2 years	−0·132	0·088	2·26	0·140	55	1
(b) Experience = 3–5 years	0·017	0·109	0·02	0·900	38	1
(c) Experience = 6–11 years	−0·036	0·109	0·11	0·700	25	1
(d) Heterogeneity among slopes	–	–	0·62	0·500	118	2
(e) Slope trend	–	–	2·04	0·140	118	1
Females						
(f) Experience = 0–2 years	−0·070	0·125	0·31	0·500	41	1
(g) Experience = 3–5 years	0·234	0·189	1·54	0·200	27	1
(h) Experience = 6–11 years	0·431	0·188	5·26	0·039	15	1
(i) Heterogeneity among slopes	–	–	2·04	0·140	83	2
(j) Slope trend	–	–	4·06	0·047	83	1

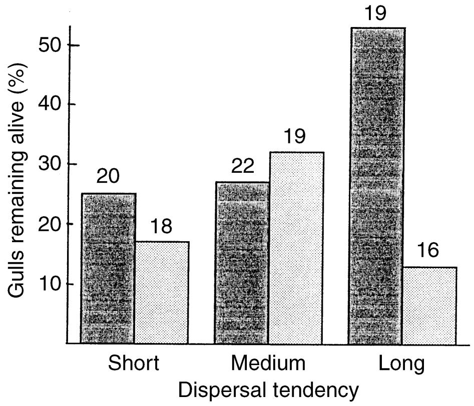

Fig. 6. Proportion of western gulls alive in 1994 as related to three categories of natal dispersal distance (males = dark bar; females = light bar). Divisions made on the basis of approximate 33% quantiles for natal dispersal distance of each sex (see Fig. 2). Values above bars are sample sizes.

males or among females (Table 6d and i). However, slope trend, the tendency for slopes relating fledging success to NDD to show increasing or decreasing trends when compared among experience groups (a test with 1 d.f. in the numerator), indicated that the relative increase in fledging success with increase in NDD became significantly greater as experience increased in females (Table 6e). Thus, the relationship between NDD and fledging success became increasingly positive as females became increasingly experienced breeders. Males showed the same trend in slope, but this was not significant ($P = 0{\cdot}14$, Table 6j).

In the preceding analyses, the effect of NDD on reproductive success among three categories of breeding experience was examined to address the question: 'Does the relation between NDD and breeding reproductivity vary with breeding experience?' The increasingly positive relationship between NDD and fledging success with increased experience observed in females could reflect a decline in fledging success with experi-

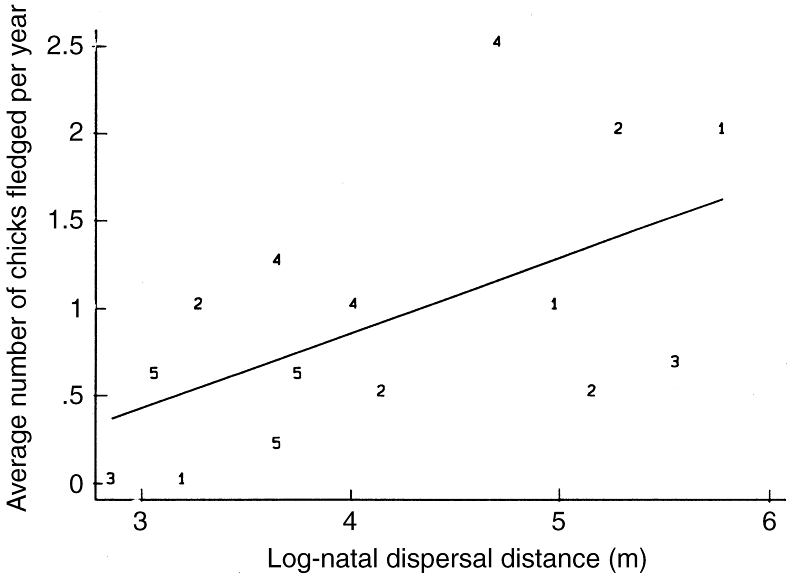

Fig. 7. Average number of chicks fledged per breeding attempt in relation to log-natal dispersal distance in experienced (previous breeding experience = 6–11 years) female western gulls, including line of best fit. Numbers denote number of breeding seasons (n) during which fledging success was monitored for a given female; regression analysis was weighted by $n^{0\cdot5}$.

ence among more philopatric females (those with lower NDD), and/or increase in fledging success among less philopatric females. To investigate these possibilities, the effect of experience on reproductive success between categories of NDD was examined to address the question, 'Does the effect of breeding experience on reproductive success vary with NDD?' NDD was divided into two categories, 'long dispersers' and 'short dispersers,' using the median NDD for the respective sexes as the cut-off between long- and short-disperser groups. To examine the effect of experience on reproductive success within an individual, a separate intercept but common slope for each individual who had been monitored for three or more years was calculated; those monitored for fewer than 3 years were excluded.

Among short-dispersing females, fledging success declined with increasing breeding experience within an individual (controlling for year and an individual main effect; Table 7, Fig. 8a). Fledging success was not significantly related to experience among long-dispersing females (F-test for linear trend, $P = 0\cdot2$, Fig. 8b). Hence, the increasingly positive relationship between NDD and fledging success with increased breeding experience in females resulted mainly from a decline in fledging success with increasing experience among short-dispersing females, rather than that long-dispersing females became more successful with an increase in experience. The study confirmed that the effect of experience on fledging success differed significantly with dispersal tendency among females; that is, there was a significant interaction between effects of NDD and breeding experience on fledging success [$F_{1,192} = 4\cdot71$, $P = 0\cdot032$; the model included NDD, breeding experience, and the interaction term, each with 1 d.f.; year, with 10 d.f.; and individual main effect, with 39 d.f.). Furthermore, the effect of experience on fledging success did not differ appreciably among individual females, as indicated by an insignificant interaction between experience and individual among short-dispersing females (Table 7). This last F-test used 47 d.f. in the denominator, which we believe is adequately large to test the significance of the interaction.

Fledging success did not differ significantly with experience among short- or long-dispersing males (F-tests, $P = 0\cdot7$ and $0\cdot8$, respectively). The same interactions as tested for females (the effect of NDD on fledging success depending on experience, and vice versa) were not significant when tested among males (both $P > 0\cdot8$).

Cumulative number of chicks fledged to 1994 increased significantly with NDD among females (controlling for years of missing data; Table 8, Fig. 9). In males, the effect was in the same direction, but not significant; the difference in slopes between sexes was not significant (Table 8). For the longest dispersing females (to 20%ile), cumulative chicks fledged averaged 8·52 (+1·44 SE); for the shortest dispersing females (lowest 20%ile) cumulative number of chicks fledged averaged 4·25 (+1·45 SE).

DOES NESTING ADJACENT TO A RELATIVE AFFECT REPRODUCTIVE SUCCESS?

Reproductive parameters of sons/brothers nesting adjacent to their living fathers/brothers differed insignificantly from reproductive parameters of sons nesting adjacent to the territories of their dead fathers (Table 9). However, results for each of the five par-

Table 7. Multiple regression model for number of chicks fledged per breeding attempt (the dependent term) as related to breeding experience among short-dispersing female western gulls. The effect of experience was not significant for long dispersers (see text). The model includes the categorical term 'individual' (ring number), including 23 females. Fledging success of all individuals was monitored during at least 3 years. The 'adjusted for' column refers to terms included in the model (main effects) when assessing the effect of a primary term. *F*-values refer to including the term in the full model in the case of those having a significant effect, and adding the term to the full model in the case of rejected terms. Terms with more than one component, separated by •, indicate interactions between component terms. Year refers to year of breeding; d.f. refers to numerator d.f. in *F*-test. Sample size was 103 observations on 23 females

Primary term	Adjusted for	d.f.	Coefficient	SE	*F*-value	*P*-value	Adjusted $R^2 \times 100$
Model $F_{33,69} = 2{\cdot}75$, 56·8% of variance explained							
Experience	Year, individual	1	3·62	1·29	7·83	0·007	4·9
Year	Individual, experience	10	–	–	3·14	0·002	21·4
Individual	Year, experience	22	–	–	1·78	0·037	32·0
Rejected terms:							
NDD	Individual, year, experience	1	4·64	4·74	0·94	0·300	0·0
Indiv. • experience	Individual, year, experience	22	–	–	0·63	0·800	7·4

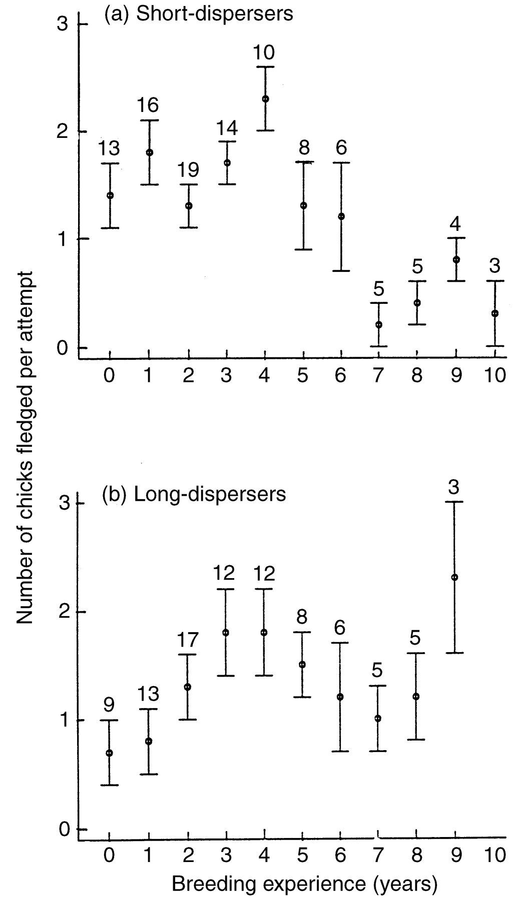

Fig. 8. Number of chicks fledged per breeding attempt for (a) short-dispersing and (b) long-dispersing female western gulls, with respect to breeding experience. Shown are the means (dots) ± one standard error (vertical bars) above and below the mean. Numbers above bars are number of attempts.

ameters were in the direction favouring nesting adjacent to a living relative; for example, males nesting adjacent to a living father or brother fledged on average 26% more young per breeding attempt than did males nesting adjacent to the territory of their deceased father (Table 9). Note that with regard to laying date, higher fitness accrues to those breeding earlier (Spear & Nur 1994). A repeat of this part of the present study is warranted, using larger samples.

Discussion

Male western gulls were more philopatric to natal sites than were females, a pattern widespread among birds (Greenwood 1980). A weaker philopatric tendency in females was to have been expected because female prebreeders significantly outnumber prebreeder males (Spear *et al.* 1987; see also Hunt *et al.* 1980), and therefore females operate under greater constraints simply to recruit. Both sexes displayed significant relationships between natal dispersal distance and fitness components, however, the relationships differed markedly between the sexes. In fact, other than prospecting distance among prebreeders, none of the variables related significantly to natal dispersal distance in one sex were significant in the other.

RELATION BETWEEN NATAL PHILOPATRY AND FITNESS IN MALES

More philopatric males had hatched earlier in the breeding season, a trait associated with higher fitness during the prebreeding period, indicated by higher post-fledging survival rate and recruitment probability, and probably higher dominance rank among early hatched individuals (Spear & Nur 1994). More philopatric males settled in areas of the colony where nesting density and nest cover were high (and where fledging rate per nest was higher compared to areas of lower nesting density during 1972–83; Penniman *et*

Table 8. Linear multiple regression model for cumulative number of young fledged (the dependent term) as of 1994, as related to natal dispersal distance (NDD; log-transformed) and sex of western gulls. Terms with more than one component, separated by •, indicate interactions between component terms. Sample *n* was 57 males and 41 females. All numerator d.f. = 1

Primary term	Adjusted for	Coefficient	SE	*F*-value	*P*-value
Males: Model $F_{2,54} = 0{\cdot}65$, 2·3% of variance explained					
NDD	Years of missing data	0·51	0·627	0·66	0·400
Years of missing data	NDD	0·47	0·528	0·40	0·500
Females: Model $F_{2,38} = 2{\cdot}66$, 12·3% of variance explained					
NDD	Years of missing data	1·52	0·732	4·31	0·045
Missing data	NDD	– 1·47	0·855	2·94	0·094
Interaction:					
Sex • NDD*	Years of missing data	–	–	1·65	0·200

*d.f. = 1,94.

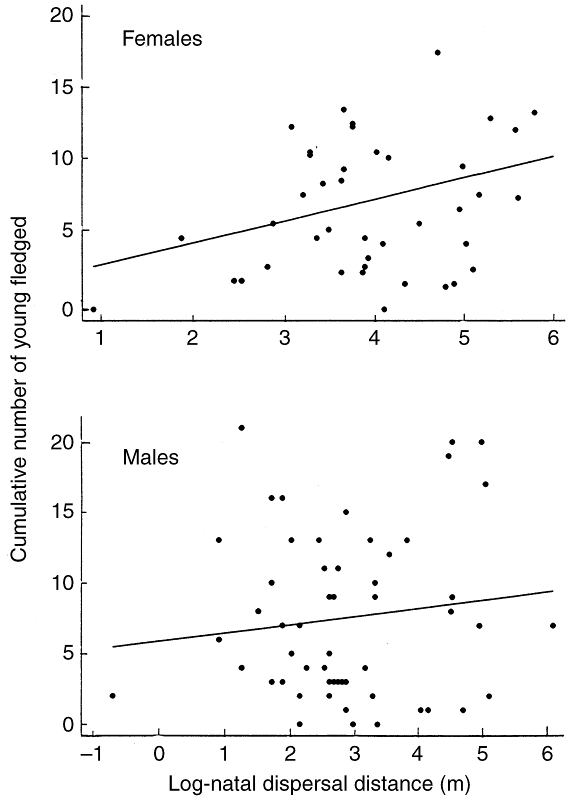

Fig. 9. Cumulative number of young fledged by female and male western gulls from recruitment through 1994 in relation to log-natal dispersal distance. Also shown are lines of best fit.

al. 1990). More philopatric males also recruited at ages more closely approximating the population norm (Spear *et al.* 1995; i.e. when aged 4–6 years), whereas less philopatric recruits were either very young (3-years-old) or older than 6 years, suggesting anomalous behaviour. Yet, for males, there was no significant relation of natal dispersal tendency to the overall fitness measure, cumulative number of chicks fledged for the period 1982–94. (Note that the measure of lifetime reproductive success in the present study was incomplete because 33% of the males were alive in 1994.) The lack of a marked relationships to the overall fitness measure was the result of two counteracting trends: (i) an insignificant trend ($P = 0{\cdot}14$) for more philopatric males to fledge more young per attempt during the first 3 years of breeding; and (ii) from the year of recruitment onward, male survival decreased significantly as philopatry increased. Indeed, males still alive in 1994 included twice as many long-dispersers as short-dispersers (10 vs. 5; Fig. 6). Thus, differences in lifetime fecundity will only be accentuated in favour of less philopatric birds.

The above suggests that at least two conflicting selection pressures were acting on males representing the two cohorts (1979–80) of western gulls. The first is selection favouring high philopatry because gulls hatching early in the season (who demonstrated higher philopatry than gulls hatching later) also demonstrate higher survival to breeding age (Spear & Nur 1994). The second is selection favouring low philopatry through better survival of breeders that disperse longer distances. The poorer survival of the more philopatric breeding males also suggests that, under the current conditions, philopatry among male western gulls may not be adaptive. This result was unexpected for two reasons. First, up to the time of breeding, more philopatric males were characterized by phenotypes suggesting that they were the more dominant, fit individuals; and secondly, the philopatric tendency among male western gulls is very strong (for comparison with other species, see Greenwood 1980).

Changes in environmental conditions from those during which philopatry evolved may, at least in part, be responsible. The present breeding population is probably larger than ever before because of extirpation of pinnipeds from extensive areas now occupied by nesting gulls (Ainley & Lewis 1974). At the same time, variation in annual food supply has a strong effect on reproductive performance of these

Table 9. Effect in males of nesting adjacent to *living* fathers/brothers vs. nesting adjacent to the territories of their *dead* fathers, measured relative to variation in five parameters of breeding performance, averaged for each gull. Laying date = Julian date (1 = 1 January). Sample sizes were 10 males (with 19 breeding attempts) nesting adjacent to territories of their dead fathers, and 7 males (with 15 breeding attempts) nesting adjacent to living fathers/brothers. *P*-values report results of Mann–Whitney *U*-tests

Primary term	Father/brother living $X \pm$ SE	Father dead $X \pm$ SE	*P*-value
Laying date	129·60 ± 2·700	131·60 ± 1·100	0·2
Clutch size	2·86 ± 0·143	2·80 ± 0·133	0·8
Number of young hatched per attempt	2·57 ± 0·202	2·07 ± 0·290	0·2
Number of young fledged per attempt	1·68 ± 0·357	1·33 ± 0·331	0·4
Young fledged per egg laid	0·58 ± 0·130	0·45 ± 0·108	0·4

gulls (Sydeman *et al.* 1991a), and food limitation among adult males was indicated by the significant effect of annual variation in food supply on their ability to recruit into the breeding population (Spear *et al.* 1995).

More recent developments affecting food supply of the gulls studied included: (i) three of the five refuse landfills most important to western gulls feeding in the San Francisco Bay region (98% of all adult Farallon western gulls who fed on refuse during the breeding season fed at the five locations during 1978–81; Spear 1988) were relocated inland, outside of the foraging range of these gulls, during the early to mid-1980s; and (ii) the occurrence of a series of years (1989–94) in which oceanic food supply was poor, having an impact on many species of seabirds on the Farallones, including a substantial decline in reproductive success of western gulls (unpublished data). Oceanic foods (small fishes, squids, and Euphausiids) composed 60–80% of the food fed to young western gulls each year during 1971–83 (Penniman *et al.* 1990).

The persistence of poor oceanic feeding conditions for 6 years was unprecedented. Prior to the mid-1980s, reproductive success of seabirds on the Farallones indicated that food supply was favourable in 3 of every 4 years from 1968 onward, and probably during most of the 20th century (see Bolin & Abbott 1963; Ainley & Lewis 1974; Ainley & Boekelheide 1990).

Lower survival among the more philopatric males is consistent with the view that they pursued a more costly reproductive strategy (reviews on costs of breeding in Williams 1966; Stearns 1976; Nur 1988; Linden & Moller 1989; Gustafsson & Part 1990; Korpimaki 1992). We suspect that in the past, under more favourable feeding conditions, philopatry was adaptive, and that under such conditions, the high degree of philopatry noted in this study was evolved. We suggest that under favourable feeding conditions, more philopatric males were able to gain a selective advantage over less philopatric males by recruiting into high density areas with favourable nesting cover, and by making a strong reproductive effort early in life, whereby they enhanced their reproductive output. If the current conditions persist, in which selection is apparently acting against philopatry, it is to be expected that this gull population should become less philopatric. This could lead to lower nesting density and to a decrease in population size on the Farallones if decreased philopatry led to emigration.

RELATION BETWEEN NATAL PHILOPATRY AND FITNESS IN FEMALES

Consistent with the males, philopatry to the natal site was well developed among female western gulls (see Greenwood 1980; for comparison). This was unexpected because, as in males, philopatry did not appear adaptive. Reproductive success, as a function of natal dispersal distance, was similar among females having breeding experience of less than 6 years, but thereafter the number of young fledged per attempt declined among more philopatric females, whilst that of less philopatric females remained stable. The overall result was that less philopatric females produced significantly more young during the 15-year study period.

Previous work on larids (Coulson & Thomas 1985; Pyle *et al.* 1997) and other species (Otariids, Sydeman *et al.* 1991b) indicated that a cost of reproduction can be manifest as decreased reproductive success with increase in the number of cumulative reproductive attempts. Along these lines, the decrease in reproductive performance among the more experienced, more philopatric female western gulls compared to the more experienced, less philopatric females, suggests that the more philopatric females may have pursued a more costly breeding strategy during their earlier years of breeding. However, lack of relation between dispersal distance and any of the factors including hatching date of recruits, recruitment age, habitat quality, nesting density, or survival probability, provided little insight into possible mechanisms whereby less philopatric females gained a fitness advantage. This subject requires further investigation.

WHY BE PHILOPATRIC TO THE NATAL SITE?

Western gulls initially prospected near to their natal sites, but subsequently prospected farther from them each year that they did not recruit. These results suggest that they preferred to be philopatric, and that reduced philopatry in some was due to an inability to recruit into preferred areas.

The apparent preference for natal philopatry in western gulls is of interest because of lack of evidence that this behaviour was adaptive. Theories as to why philopatry might be adaptive in avian species include benefits from local experience with resources, predators and conspecifics, and increase in competitive ability in a familiar area (see Introduction). However, none of these factors would be likely to apply to western gulls in the Farallones colony. Prospectors can easily assess nesting habitat with overflights and, thus, prior local experience is probably of little value. Also, it is unlikely that many prospectors had gained on-site experience with local habitat other than that at the natal site itself because adults allow only their young on their territories. Experience with predators is unlikely because the only important predators in the Farallones colony (conspecifics) forage in an unlocalized, unpredictable manner; see Parsons (1978) for similar findings in herring gulls [*Larus argentatus* (Pont.)]. It is unlikely that there was much difference in prospector's familiarity with potential nesting locations because, early in life, almost all prospectors began prospecting close to their natal sites. In contrast, the results from the present study were consistent with a positive effect of kin selection (see Greenwood *et al.* 1979a; for similar results) on reproductive performance, but were inconclusive due to small sample size.

Other than the possible effect of kin selection, selection for natal philopatry in western gulls could result from reduced competition for breeding sites within the colony; for example, if most prospectors converged on a few particularly favourable areas, competition would be exceedingly intense and deleterious to many because of lost time and energy, and possible injury. Yet another possible explanation, postulated by Oring & Lank (1984), is that the mere existence of an individual is a good indication that its natal area was favourable for reproduction.

Conclusion

In this study, there was weak evidence suggesting possible benefits associated with high philopatry; that is, the tendency for reproductive success early in life to be greater among more philopatric males ($P = 0{\cdot}14$). This insignificant result should not be construed as conclusive evidence that such benefits were absent. The sample size was small (98 individuals monitored for reproductive success) for a study of natural selection, with the result that only the most potent costs and/or benefits of philopatry were likely to be statistically detectable. The quandary faced by this, and other, studies of natural selection in the wild is that subtle, more difficult to detect fitness effects (Graves 1991) can still be of major importance in the evolution of life history strategies (Nur 1988). Ecologists must be wary of making Type II errors (assuming the null hypothesis is true when it is not), but this is especially problematic in field studies of evolution where large sample sizes are usually unattainable.

Results from the present study demonstrated, instead, costs associated with natal philopatry: for males, a reduction in survival of breeders; for females, a reduction in reproductive success among more experienced individuals and a reduction in total number of chicks fledged. These results indicated that natal philopatry was not adaptive in Farallon western gulls during the 15 years of this study. This is paradoxical because natal philopatry seems highly developed in this population, compared to other bird species (Greenwood 1980). We hypothesize that this unexpected result was due to the recent deterioration in food supply (post-1970s) in the Gulf of the Farallones and that this deterioration had a more adverse effect on more philopatric western gulls compared to less philopatric ones. Under this hypothesis, relative advantages and disadvantages between the two life history strategies (high vs. low philopatry) could lead to selective equilibrium, depending on periodicity in change of environmental conditions.

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