

RE-EVALUATION OF ADULT SURVIVAL OF BLACK-HEADED GULLS (*LARUS RIDIBUNDUS*) IN PRESENCE OF RECAPTURE HETEROGENEITY

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ABSTRACT.—An adequate knowledge of the growth rate of a population often is needed in conservation biology and population management. In long-lived species, annual adult survival is the demographic parameter that has the strongest influence on population growth rate. Adult survival often is estimated by capture-recapture methods under the restrictive assumption that all individuals in a given group have the same survival and recapture probabilities. Violation of this assumption, i.e. heterogeneity among individuals, tends to bias survival estimates. In particular, heterogeneous capture probabilities independent of survival probabilities tend to negatively bias survival estimates. However, a cautious use of capture-recapture methods allows recognition of the problem and an accurate estimation of survival. We estimated adult survival in a population of Black-headed Gulls (*Larus ridibundus*) breeding in central France based on resightings of banded birds. The estimated survival was lower in the year after the first resighting than afterwards. We did not find any substantial biological explanation for this result (in particular, it was difficult to connect it with the existence of prospecting individuals). However, heterogeneity in the resighting probability, which is very likely in this population, could explain why apparent survival seemed lower in the year immediately after the first resighting. The higher value of the survival estimate (0.90) when capture-rate heterogeneity is accounted for is discussed relative to the growth regime of the population and habitat instability. Received 20 November 1996, accepted 9 June 1997.

ASSESSING THE DYNAMICS OF A POPULATION or a group of individuals is of primary importance both in evolutionary biology (Stearns 1992) and in conservation biology (e.g. Doak 1995). In long-lived species, adult survival probability is the key parameter to which the population growth rate is the most sensitive (Lebreton and Clobert 1991). Indeed, sensitivity of the multiplication rate of the population to fecundity drops rapidly with generation time, whereas that to survival remains constant (Lebreton and Clobert 1991). For instance, in the Northern Spotted Owl (*Strix occidentalis caurina*), a 1% decrease in adult survival is sufficient to induce a 1% change in the predicted multiplication rate of the population, whereas a 54% decrease in fecundity is needed to induce this change (Lande 1988). A similar imbalance in sensitivity between adult survival and fecundity has been proposed in Herring Gulls (*Larus argentatus*; Migot 1992).

Adult survival is well studied in larids. Early estimates were obtained from analyses of individuals banded as chicks and later found dead (e.g. Kadlec and Drury 1968). However, such estimates may be affected by many different biases (Anderson et al. 1985, Francis 1995). Consequently, many early estimates of survival in gulls are inconsistent with observed growth rates of the populations studied, as noted by several authors (e.g. Ludwig 1967, Kadlec and Drury 1968, Lebreton and Isenmann 1976).

Recapture or resighting data, frequently obtained during long-term population studies, are more reliable. Many such studies have considered that the recapture probability was close to 1.0 and thus have equated return rate and survival probability (e.g. Coulson and Wooller 1976, Spear et al. 1995). This practice induces a bias in the estimation of survival probabilities (Nichols 1992, Clobert 1995). However, survival and capture probabilities can be estimated separately from recapture or resighting data using appropriate capture-recapture models (Lebreton et al. 1992). Moreover, the effects on survival and capture probabilities of factors such

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as age or sex can then be assessed (Lebreton et al. 1992).

An important assumption of most current capture-recapture models is that all individuals have the same survival and recapture probabilities (Carothers 1973, Lebreton et al. 1992). This is the homogeneity assumption. Its violation (i.e. heterogeneity) is known to bias capture-recapture estimates of population size (Carothers 1973, Pollock 1982, Hwang and Chao 1995). The effect of heterogeneity of capture on survival estimates is limited when capture probabilities are high (Carothers 1973, Lory et al. 1987, Lebreton 1995). However, this type of heterogeneity may be troublesome in other cases (e.g. Buckland 1982). For the extreme situation of transient individuals with zero probability of reobservation, Pradel et al. (1997:figure 1) gave the magnitude of the bias as a function of the proportion of transients in the population. Fortunately, alternative model structures allow heterogeneity to be accounted for, at least in part (Francis and Cooke 1993, Pradel 1993, Pradel et al. 1997).

Using capture-recapture methodology, we studied survival of adult Black-headed Gulls (*Larus ridibundus*) based on resightings of banded individuals in a large colony in central France. We compared survival of males versus females and of residents versus immigrants in the colony. We then connected the estimated survival with dispersal propensity or prospecting behavior. Because we suspected strong heterogeneity in our data, we investigated by simulation the effect of heterogeneity in capture probabilities on the estimation of survival. We then accounted for it using an adequate model structure that induced a marked upward shift in the probability estimates of annual survival. We discuss this shift as it relates to the demography of the population and to habitat instability.

METHODS

Study area and data collection—We collected data on individual capture-recapture histories of Black-headed Gulls from 1976 to 1993. The population breeds in the Forez plain 60 km west of Lyon in central France. Each year, several colonies occupy man-made ponds spread over farmland. The largest one, La Ronze (Craintilleux, Loire, 45°35'N 4°14'E), attracts about 4,000 breeding pairs each year. Gulls breed on vegetation growing in the pond. The study

area and the Black-headed Gull population are described in Lebreton and Landry (1979). In particular, the vegetation used by the Black-headed Gulls is made up of dense beds (see Lebreton and Landry 1979).

Black-headed Gulls have been banded by two different methods. First, at the beginning of the breeding season each spring (March to April), adults were trapped with a cannon net on feeding grounds within a few kilometers of La Ronze. They were banded and sexed (based on measurements; Allainé and Lebreton 1990) but could not be aged. Second, in late May and early June, preledged young were banded in various colonies (see Lebreton and Landry 1979, Lebreton 1981); these young could not be sexed. Every year, banded birds were resighted on the La Ronze colony from a floating hide (Lebreton 1987). The dense beds used by Black-headed Gulls make resightings increasingly difficult as individuals breed more toward the center of the vegetation islets. Because virtually all individuals captured with the cannon net have brood patches, we assumed that most of the birds resighted in the colony were in breeding condition (Beer 1961). Among birds banded as young, both natives and immigrants of known age have been resighted. From 1976 to 1993, 29,333 young and 1,921 adults have been banded, and 1,090 different individuals have been resighted at least once as breeders.

Twenty-two individuals banded as chicks and resighted in the colony also were captured with the cannon net. They were included in the data set of birds banded as young, and the event of recapture with the cannon net was ignored.

We were interested only in the birds breeding at La Ronze. Thus, we considered only the local recapture histories of individuals resighted at least once as a breeder at this colony, from their first resighting onwards, independently of their age. This procedure excluded birds captured as breeders in other colonies, as well as birds banded as young and breeding elsewhere. Because the resightings were done by reading band numbers at distance, there was no bias due to disturbance. Thus, trap-dependence in the restricted sense (Pollock 1982) was unlikely.

We split the cannon-net data set according to sex in order to test for possible sex-dependence of survival or recapture probability, and split the data of birds banded as young according to their origin. Four data sets were thus available: (1) birds banded as young in the study colony (residents; $n = 643$), (2) birds banded as young in another colony (immigrants; $n = 156$), (3) cannon-netted adult males ($n = 230$), and (4) cannon-netted adult females ($n = 61$).

Analysis of adult survival probability.—Data were analyzed following capture-mark-recapture methodology (Lebreton et al. 1992) with programs RELEASE (Burnham et al. 1987) and SURGE (Pradel and Lebreton 1991). A capture-recapture analysis is

analogous to an analysis of variance. One starts from a global model including the factors suspected to affect survival and capture probabilities. First, the fit of the global model is assessed. The starting model often is the time-dependent model of Cormack (Cormack 1964, Jolly 1965, Seber 1965) applied to each data set separately. In this model, denoted $[\phi_{t,r_g}, p_{t,r_g}]$ (see Lebreton et al. 1992), survival and capture probabilities vary with group (immigrants, residents, males, females) and with year, including interactions among these variables (star notation). However, when this model does not fit the data, several generalizations are available. We will consider the generalization to two classes of relative age (see Fig. 1). This generalization has been introduced by Brownie and Robson (1983) for just one group and can be denoted as $[\phi_{a,t}, p_t]$ following Lebreton et al. (1992), with a for relative age (with two categories) and t for time. We will denote it alternatively when needed as $[\phi_{i,t}^*, \phi_{i,t}, p_t]$. The latter notation, contrary to the former, has the advantage of covering models with separate structures for the first-year and after-first-year survival. For instance $[\phi^*, \phi_{i,t}, p_t]$ stands for a model with constant first-year survival, subsequent time-dependent survival, and time-dependent capture probabilities, which does not enter the usual notation.

We used a modified version of program RELEASE (Pradel 1993) to test the fit of these models. The complete test involves four components that are expected to be nonsignificant under the time-dependent model applied to each data set separately (model $[\phi_{t,r_g}, p_{t,r_g}]$). Because each component tends to be sensitive to different effects, possible departures from the time-dependent model, such as age effect on survival or trap effect, may be detected. In particular, test 3.SR tests if individuals resighted for the first time in year i have the same probability of being resighted in subsequent years as those first resighted before year i . The significance of test 3.SR suggests the use of a relative age effect on survival, i.e. of $[\phi_{a,t,r_g}, p_{t,r_g}]$; equivalent notation $[\phi_{i,t}^*, \phi_{i,t}, p_{t,r_g}]$.

Once a satisfactory general model was identified, progressively simpler models were fitted with program SURGE. We obtained the relative deviance of each model and the estimates of survival and resighting probabilities. Model selection was based on minimization of Akaike's Information Criterion (AIC) with a small number of likelihood-ratio tests for specific hypotheses (see Lebreton et al. 1992).

We chose an initial model based on general goodness-of-fit tests for the four data sets. Using program SURGE, we first analyzed the data on birds banded as young and compared residents versus immigrants. Then we simultaneously analyzed these two data sets and those concerning birds captured with the cannon net, split into males and females.

Simulation of heterogeneity in resighting probability.— To test whether heterogeneity in resighting proba-

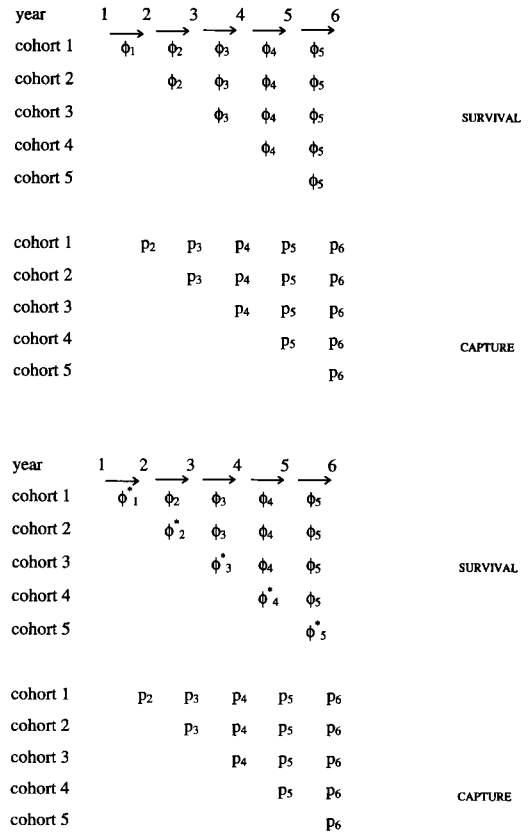


FIG. 1. Comparison of the time-dependent model (upper matrix; Cormack 1964) and the time-dependent model with two classes of relative age (lower matrix; Brownie and Robson 1983) for six years of capture and one group. ϕ_i = survival probability from year i to year $i + 1$; p_i = recapture probability from year i ; ϕ_i^* = survival probability from year i to year $i + 1$ for animals first resighted in year i ; and cohort i = animals first resighted in year i . In the second model, initial survival over the interval immediately following the first resighting in the colony is allowed to differ from subsequent survival.

bilities could lead to the observed relative age effect on survival, we assumed that there were two sets of individuals, both faithful to their breeding area, one made up of individuals breeding on the center of islets (low resighting probability [p_1]), and one of individuals breeding on the edge of islets (high resighting probability [p_2]). The proportions of the two categories were α and $1 - \alpha$, respectively. We simulated capture-history samples, combining the two subgroups. We used the following parameter values in the simulations: (1) survival probability was the same for all individuals, equal to the value for after-first-year individuals estimated from the real data

TABLE 1. Goodness-of-fit tests for models with: (1) time effect on survival and recapture probabilities ($[\phi_{\nu}, p_i]$); and (2) time and age effects on survival, time effect on recapture probability ($[\phi_{a2\nu}, p_i]$). Test 3.SR tests the relative age effect on survival.

	$[\phi_{\nu}, p_i]$			$[\phi_{a2\nu}, p_i]$			Test 3.SR		
	X ²	df	P	X ²	df	P	X ²	df	P
Males	63.1	53	0.16	45.4	45	0.46	17.7	8	0.020
Residents	67.7	58	0.18	41.1	49	0.88	26.6	9	0.002
Total	130.8	111	0.10	86.5	94	0.70	44.3	17	0.001

set; (2) the number of years in the simulated data set was identical to the real one (i.e. 16); and (3) at each occasion, the total number of newly sighted individuals was the same as in the real data set. In accordance with the previous assumptions and parameterization, the proportion π_1 of newly sighted individuals with a low resighting probability was set at:

$$\frac{\alpha p_1}{\alpha p_1 + (1 - \alpha)p_2} \quad (1)$$

The simulations were run using program RELEASE (Burnham et al. 1987). We adjusted the values of p_1 and p_2 in order to obtain similar survival and resighting probability estimates under the selected model as those derived from the real data set, and then examined the similarity of the final values.

RESULTS

Initial model.—The tests could validly be run only for the two larger data sets: males and residents. In both cases, only test 3.SR was significant (Table 1). Our examination revealed that at each occasion, more animals than expected among the newly marked ones were never seen again, and the same tendency occurred for females and immigrants. Thus, although model $[\phi_{\nu}, p_i]$ had to be rejected, the model with two age classes ($[\phi_{t+a}, p_i]$) appeared to describe the data adequately for all data sets. This model

specifies that the survival of birds in the year following their first resighting may differ from that of other individuals. This does not mean that animals of different real age have different survival probabilities. Indeed, the data sets included birds of unknown age (cannon-netted ones) and birds of different known ages (banded as chicks).

Immigrants versus residents.—Model selection led to $[\phi^*, \phi, p_i]$ (Table 2). According to this model, there was a relative age effect on survival probability and annual variation of resighting probability. The survival and resighting probabilities did not differ significantly with the origin of the individuals. Therefore, we pooled the data from these two groups in subsequent analyses.

Adults banded as young versus cannon-netted adults.—Model selection led to $[\phi^*, \phi, p_{t+g}]$ (Table 3). According to this model, the survival probabilities in the year following the first resighting differed from those afterwards, but neither differed significantly among groups (i.e. banded as chicks, males, females). The survival probability estimate in the first year after initial resighting was $\phi^* = 0.59$ (95% confidence interval 0.51 to 0.67). After the first year, it was much higher, $\phi = 0.90$ (0.86 to 0.92). Resighting probability was time- and group-dependent.

TABLE 2. Model selection for survival and resighting rates for residents versus immigrants. ϕ^* = survival rate the year after first resighting; ϕ = survival rate in the following years; p = resighting rate; t = time in years; g = groups (resident, immigrant).

Model	Deviance	df	AIC ^a	Tests of hypotheses
(1) $[\phi^*_{t+g}, \phi_{t+g}, p_{t+g}]$	1,825.21	60	1,945.21	
(2) $[\phi^*_{t+g}, \phi_{t+g}, p_i]$	1,839.40	49	1,937.40	p time dependent (2 vs. 1); $P = 0.22$
(3) $[\phi^*_{\nu}, \phi_{\nu}, p_i]$	1,850.89	33	1,916.89	ϕ^* and ϕ group constant, time dependent (3 vs. 2); $P = 0.78$
(4) $[\phi^*_{\nu}, \phi_{\nu}, p_i]$	1,873.82	17	1,907.82	ϕ^* and ϕ time constant, group dependent (4 vs. 2); $P = 0.35$
(5) $[\phi^*_{\nu}, \phi_{\nu}, p_i]$	1,874.59	16	1,906.59	ϕ time and group constant (5 vs. 4); $P = 0.13$
(6) $[\phi^*_{\nu}, \phi_{\nu}, p_i]$	1,874.63	15	1,904.63	ϕ^* time and group constant (6 vs. 5); $P = 0.84^b$
(7) $[\phi^*, \phi, p]$	1,925.17	3	1,931.17	p time constant (7 vs. 6); $P < 0.0001$

^a Akaike's Information Criterion.

^b Selected model based on lowest AIC value.

TABLE 3. Model selection for survival and resighting rates for all adults banded as young and cannon-netted males and females. ϕ^* = survival rate the year after first resighting; ϕ = survival rate in the following years; p = resighting rate; t = time in years; g = groups (adults banded as young, cannon-netted males, cannon-netted females); g' = groups (cannon-netted males and adults banded as young pooled, cannon-netted females).

Model	Deviance	df	AIC ^a	Hypotheses
(1) [$\phi^*_{t'g'}$, $\phi_{t'g'}$, $p_{t'g}$]	2,839.74	86	3,011.74	
(2) $\phi^*_{t'g'}$, $\phi_{t'g'}$, $p_{t'g}$]	2,859.17	67	2,993.17	Additive effects of time and group on p
(3) [$\phi^*_{g'}$, $\phi_{g'}$, p_{t+g}]	2,919.88	23	2,965.88	Survival not time dependent
(4) [$\phi^*_{g'}$, $\phi_{g'}$, p_i]	2,926.97	19	2,964.97	Time effect, no group effect on p
(5) [$\phi^*_{g'}$, $\phi_{g'}$, p_g]	2,980.71	8	2,996.71	Group effect, no time effect on p
(6) [$\phi^*_{g'}$, $\phi_{g'}$, p_{t+g}]	2,920.09	22	2,964.09	No group effect on ϕ
(7) [ϕ^* , ϕ , p_{t+g}]	2,920.98	20	2,960.98	No group effect on ϕ^* or ϕ
(8) [ϕ^* , ϕ , p_{t+g}]	2,922.26	19	2,960.26	$p_{\text{male}} = p_{\text{young}} \neq p_{\text{female}}^b$
(9) [ϕ^* , ϕ , p_i]	2,933.97	18	2,969.97	No group effect on p

^a Akaike's Information Criterion.
^b Selected model based on lowest AIC value.

The effects of time and sex could be considered as additive ($[\phi_{a2't'g'} p_{t'g}]$ vs. $[\phi_{a2't'g'} p_{t+g}]$; $\chi^2 = 19.43$, $df = 19$, $P = 0.43$). It was also possible to consider that males and birds banded as young shared the same resighting probabilities (test of two groups [g'] against three groups model $[\phi_{a2't} p_{t+g}]$ vs. model $[\phi_{a2't} p_{t+g}]$; $\chi^2 = 1.28$, $df = 1$, $P = 0.26$; Table 3). However, males and birds banded as young were resighted significantly more often than females (model $[\phi_{a2't} p_{t+g}]$ vs. model $[\phi_{a2't} p_i]$; $\chi^2 = 11.31$, $df = 1$, $P < 0.001$; Table 3).

Factors affecting ϕ^ .*—The relative age effect on survival probability ϕ^* being significantly lower than ϕ indicated that a high proportion of birds was not seen again after their first resighting. This could be due to differences in behavior: (1) the propensity for breeding dispersal may differ for immigrants and residents; (2) individuals new to the colony may disperse following a breeding failure; and (3) some birds may have been transients.

The proportion of birds that dispersed between breeding attempts did not differ between residents and immigrants (Table 2). Moreover, the outcome of breeding attempts did not seem to influence the probability of disappearance from the colony. Specifically, ϕ^* was not significantly lower for birds seen at nests without chicks (unsuccessful breeders) than for those seen with chicks (model [ϕ^* different for successful and unsuccessful breeders] vs. model [ϕ^* no difference]; $\chi^2 = 2.57$, $df = 1$, $P = 0.11$; estimate of ϕ^* for successful individuals was lower than that for unsuccessful individuals).

The fact that many individuals were seen only once in the colony could reflect the presence of transients, i.e. individuals that do not belong to the colony. These birds may be prospectors that visit the colony before becoming established in it, either young that have not bred or adults that failed in another colony (Cadiou et al. 1994). Because young individuals are more likely to visit a colony before becoming established, they would be more prone to be seen in a colony just once. Using birds banded as chicks, we were able to study the influence of the age of individuals at first resighting on ϕ^* . We split the data on resident birds into six subgroups depending on the age at first resighting (2, 3, 4, 5, 6, ≥ 7 years). In order to maximize power, we investigated a trend in ϕ^* with age. First-year survival was not significantly dependent on age of individuals (Table 4), i.e. young residents did not disappear more often than older ones.

Effect of resighting heterogeneity on survival.—Because of the structure of the vegetation in dense beds, the only sites (nests or resting sites) accessible to observation were those located close to the vegetation edge or in open water. Although birds breeding on the edge of vegetation were easy to resight, those breeding in the center of vegetation islets could be resighted only when they were resting on an accessible site. Under the assumption of equal nest density inside and on the edge of vegetation islets, we estimated the respective proportions of the two sets of birds to be $\alpha = 0.90$, and $1 - \alpha = 0.10$.

We simulated heterogeneous data sets with adult survival equal to 0.90, i.e. the estimated

TABLE 4. First-year survival (ϕ^*) of residents resighted for the first time at different ages. Residents were subdivided into six groups depending on age at first resighting (2, 3, 4, 5, 6, ≥ 7 years).

Model	Deviance	df	AIC ^a	Hypotheses
$[\phi^*_{age}, \phi, p_i]$	1,620.81	23	1,666.81	ϕ^* different for all groups
$[\phi^*_{ageinv}, \phi, p_i]$	1,624.32	19	1,662.32	ϕ^* decreases linearly with age
$[\phi^*, \phi, p_i]$	1,624.34	18	1,660.34	ϕ^* not age dependent ^b

^a Akaike's Information Criterion.

^b Selected model based on lowest AIC value.

value from the real data set for after-first-year individuals. We then fitted the model $[\phi_a, p]$ (survival with two age classes, resighting constant over time) and adjusted the values of p_1 and p_2 in order to obtain the following results: ϕ^* close to 0.59, ϕ close to 0.90, and p close to 0.20. The resighting probabilities leading to values of ϕ^* , ϕ , and p close to the estimates were $p_1 = 0.07$ and $p_2 = 0.30$ (Table 5). The sensitivity of these results to α was fairly high, because $\alpha = 0.85$ led to too high a value of ϕ^* (values of ϕ^* , ϕ , and p equal to 0.69, 0.90, and 0.22, respectively).

DISCUSSION

Resighting probability.—Our results indicate that males were resighted significantly more often than females. This could result from a higher level of activity of males in the colony at the time of resighting (generally in the beginning of afternoon). If males were standing more often than females, e.g. because of more frequent agonistic behavior, their bands would be easier to see than the females' bands. This difference also could result from a higher breeding dispersal of females, a general rule among birds (Greenwood and Harvey 1982), implying in turn more temporary emigration

from La Ronze in females than in males. However, in order to have no effect on survival probability, emigration should be completely random (sensu Kendall et al. 1997), which contradicts with the breeding-site and group fidelity observed in most long-lived bird species (Southern 1977, Coulson and Nève de Mévergny 1992). Similarly, the lower resighting rate of females also could reflect a higher probability for them to skip one or more breeding events, as hypothesized for California Gulls (*Larus californicus*) by Pugesek et al. (1995).

The resighting probability of birds banded as chicks (i.e. unsexed) was significantly higher than that of females but not significantly different from that of males. However, we expected the chick resighting rates to be intermediate between those of adult males and females because the sample included unknown proportions of the two sexes. Two nonexclusive reasons may explain this result. First, because males were more resightable than females, the respective proportions of the two sexes in the sample of birds banded as chicks was likely to be male-biased because the sample was made up of birds seen at least once in the colony. Second, because natal dispersal in birds is female-biased (Greenwood and Harvey 1982), the sample of residents banded as chicks may have been male-biased, yielding a resighting probability close to that of males. Because most of the birds banded as chicks were residents, the sex ratio of residents breeding in the colony may have influenced the estimate of capture probability for the entire sample of birds banded as chicks.

Survival probability in the year following the first resighting.—The relative age effect on survival probability was due to the presence of an excess of individuals resighted only once. These individuals may have disappeared from the colony after their first resighting due to death or dispersal. If individuals suffered higher

TABLE 5. Estimates of survival and resighting probabilities under model (ϕ_a, p) for 10 simulated heterogeneous data sets. Survival probability was set at 0.90. The proportions of individuals "hardly" versus "easily" resightable were 0.90 and 0.10, respectively, or 0.68 and 0.32 in the resighted sample. Resighting probabilities of the two subsets were 0.07 and 0.30, respectively.

	Simulated data sets			Estimated values	
	\bar{x}	SE	95% CI	\bar{x}	95% CI
ϕ^*	0.65	0.048	0.55–0.74	0.59	0.51–0.67
ϕ	0.89	0.019	0.86–0.93	0.90	0.86–0.92
p	0.20	0.014	0.17–0.23	0.20	—

mortality after their first breeding attempt, we would have expected a higher cost among young birds. However, ϕ^* was not correlated with the real age of individuals. Moreover, this explanation was not very realistic for long-lived species in which young individuals should favor survival to the detriment of one reproductive event (Drent and Daan 1980). The independence between ϕ^* and age also did not provide evidence for the presence of young prospectors in the colony. Finally, some individuals may have dispersed after their first breeding attempt. Breeding dispersal has been noted in larids such as Black-legged Kittiwakes (*Rissa tridactyla*; Danchin and Monnat 1992), but the dispersal events were associated with breeding failure. In our case, the probability of disappearance did not differ between birds first resighted with young and those first resighted without young.

Errors in reading bands could "identify" an individual that was not present in the colony. Such individuals would disappear after their "first" sighting because two identical errors are unlikely to occur. Pradel et al. (1997) have shown that an excess of disappearances among newly sighted individuals compared with what would be expected in a homogeneous population can be estimated by $1 - (\phi^*/\phi)$, i.e. about 34%. Given that about 60% of the total observations made each year at La Ronze were first resightings, the excess of disappearances represents about 20% of the observations, yielding an error rate that seems unrealistic.

Another interpretation for the age effect on survival is the existence of heterogeneity in the capture probability of individuals. An individual with a relatively low resighting rate has a higher tendency than the average to be resighted only once. This first resighting can occur any time in its life. The excess of individuals seen only once thus will not decrease with age. As shown by the simulation study, such capture heterogeneity can account for the observed relative age effect on survival. Individuals with the lowest capture probabilities will appear as near-transients. Thus, it is not surprising that the same model structure, i.e. a relative age effect on survival, accounts for transience (Pradel et al. 1997) and for heterogeneity with low capture probability. Hence, on the methodological side, the clear message arising from our work is that heterogeneity in capture probability may have

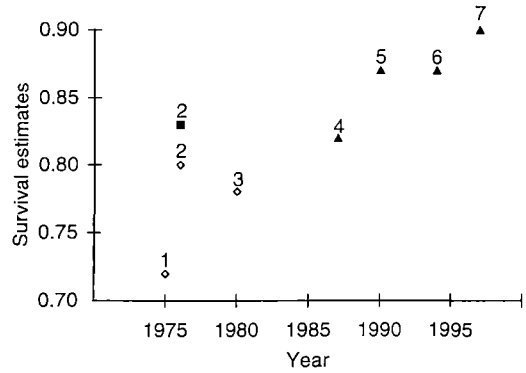


FIG. 2. Black-headed Gull survival estimates from 1975 to 1995. Open diamonds are from recovery data of different gull populations; filled square is from a life table; filled triangles are from capture-recapture data from the same gull population. 1, Flegg and Cox (1975); 2, Lebreton and Isenmann (1976); 3, Beklova and Pikula (1980); 4, Clobert et al. (1987); 5, Lebreton et al. (1990); 6, Clobert et al. (1994); 7, this study.

devastating effects, in particular when the capture probability is low. Designs that minimize this type of heterogeneity should be used; however, this is not always possible. Thus, we strongly recommend that researchers specifically test for a relative age effect in survival, in particular when the average capture probability is low. Specific powerful tests with one degree of freedom are summarized by Lebreton (1995) and Pradel et al. (1997).

Adult survival probability.—Adult survival probability did not vary according to sex or dispersal status (immigrants vs. residents). Capture-recapture studies carried out on a single site make it possible only to estimate local survival probability, i.e. the product of survival probability and probability of not having dispersed. True survival probability should be higher than the estimated value. The high value of our survival estimate (0.90) suggests that there is no (or little) dispersal of breeding gulls. Indeed, this parameter was estimated in a productive and stable colony where individuals should be more likely to be site faithful than in less productive and more unstable colonies.

Our estimate of adult survival probability is higher than all available estimates for this species (see Fig. 2). The increase in survival estimates over time may reflect a real increase in survival, or it may be due to improvement in estimation methods (Clobert and Lebreton 1991). Historically, survival estimates based on

recoveries of dead birds carried assumptions that rarely hold true, i.e. time-independent survival probabilities and age- and time-independent reporting probabilities (Anderson et al. 1985). Despite recent progress (see Freeman and Morgan 1992), the results of recovery analyses frequently are biased (see Clobert and Lebreton 1991, Francis 1995, Lebreton et al. 1995). Capture-recapture analysis allows the fitting of complex models involving dependence of variables such as age and time on survival and recapture probabilities. Consequently, models used to estimate survival are likely to provide a better fit to real data, and survival is likely to be assessed more correctly.

Survival is but one of the demographic parameters influencing the growth rate of a population. A balance between survival and other parameters, such as recruitment rate or fecundity, is needed to obtain the stability of the population we studied. Using an estimated adult survival of 0.87, previous studies have concluded that Black-headed Gulls do not attain full reproduction until at least 5 years of age (Lebreton et al. 1990, Clobert et al. 1994). Increasing the survival estimate probably would decrease the estimated recruitment rate and increase the estimated age of full reproduction. Moreover, the estimate of annual breeding success also should decrease to balance the increased survival estimate. Indeed, the annual breeding success of Black-headed Gulls in our study area recently was estimated at close to one young per pair (Prévoit-Julliard 1996) instead of 1.6 young, when a high proportion of total brood failure was not detected (Lebreton and Landry 1979, Lebreton 1996).

Recent estimates of adult survival based on capture-recapture methodology are available for several species of larids. These estimates are strikingly similar: 0.85 in Black-legged Kittiwakes (Danchin and Monnat 1992), 0.88 in Herring Gulls (Pons and Migot 1995), 0.896 in Mew Gulls (*Larus canus*; Rattiste and Lilleleht 1995), 0.915 in California Gulls (Pugesek et al. 1995), and 0.90 in Black-headed Gulls (this study). Therefore, the implications of such high survival estimates in terms of demographic stability and adjustment needed for other demographic parameters are similar for many larids. The high survival in Black-headed Gulls, once framed in this set of results, casts new light on the relationship between demography and hab-

itat preference in larids. A classic view is that short-lived larids have been able to occupy unstable freshwater habitats precisely because they are shorter lived (Siegel-Causey and Kharitonov 1990). This view is based on the following reasoning. First, many larids living in freshwater marshes (which are supposed to be among the most unstable habitats used by larids) are small-sized, belonging mostly to the "hooded" gull group (Dwight 1925). Second, based on the classic relationship between longevity and size (see Gaillard et al. 1989), these smaller-sized species tend to have reduced longevity (in particular adult survival) relative to larger gulls. Indeed, this view was consistent with many survival estimates until recently. Last, based on the r- and K-selection literature (see Pianka 1970), short-lived species are better adapted to unstable habitats than longer-lived species. This view seemingly was confirmed by the impressive longevity of members of the Procellariiformes (see Jouventin and Weimerskirch 1991) that inhabit stable habitats.

We note, however, that habitat instability clearly influences fecundity and not survival. For example, the flooding of a marsh will not increase the mortality of adults, and predation will be more of a deterrent to chicks than to adults. Thus, in evolutionary terms, larids occupying habitats in which their reproduction is unpredictable are faced with a variable reproductive output over time. In the context of a classic survival-fecundity tradeoff, "it pays to reduce reproductive effort to live longer and reproduce more times" (Stearns 1992:168). Our results open the way to a new interpretation of the demographic tactics of small-sized larids in unstable habitats, i.e. that of a bet-hedging situation. Clearly, more reliable estimates of survival for such species, and a fully comparative approach (see Harvey and Pagel 1991), are needed to further explore this interpretation. An alternative view in the same framework is that the demography of larids results from a preadaptation to habitats in which reproduction is unpredictable, rather than an adaptation to current habitat conditions.

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